BASIC ISSUES IN GREAT LAKES RESEARCH

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1. INTRODUCTION

PURPOSE AND SCOPE OF WORKSHOP

Large lakes offer issues and opportunities for research that can be duplicated neither by marine investigations nor by studies of small lake basins. World-wide, large lakes exhibit a broad range of physical and chemical circumstances, as well as diverse and different biological communities. The ecosystems have been incompletely studied historically and much remains to be learned. Careful planning now can speed future progress and promote lines of inquiry toward conceptual syntheses.

In addition to research issues, practical questions arise about the availability and accessibility of equipment and facilities for investigations of large lakes. Special and sophisticated logistical support is necessary to study large lakes. Requirements for vessels and facilities exceed the means of individual investigators and practical needs for coordination exist. For all of these reasons scientists engaged or interested in studies of basic physical, chemical, and biological limnology in large lakes should identify research topics of common interest.

In response to the needs of the research community, a workshop on Great Lakes research issues was held in 1986, sponsored by The University of Michigan and the U.S. National Science Foundation. The workshop participants identified critical basic science issues and recommended research directions.

ORGANIZATION AND OPERATION OF THE WORKSHOP

Organization of the workshop was the responsibility of a Steering Committee, composed of aquatic scientists from the U.S. and Canada. Steering Committee members identified the list of invited participants and background speakers, and they prepared the preliminary charges to the working groups.

The workshop proceeded as follows. On Day 1, five speakers introduced and reviewed the issue areas. The papers based on these talks are Appendix B of this report. Afterwards, participants met in working groups to address charges drafted by the Steering Committee about topics that transcend traditional discipline boundaries. The reports from these groups are Chapters 3 to 6. On Day 2 the participants assembled along discipline lines to address topics related to gaps in basic knowledge, facilities, equipment and techniques which are necessary to implement the study of priority issues. The reports of these groups are summarized in Appendix A.

REPORT DOCUMENT

This document represents the findings of workshop participants on the states of knowledge, immediate issues, and recommendations for future investigation. Although relatively independent at the working level, the various groups agreed on many essential issues, and these constitute the summary recommendations (Chapter 2). This report is intended to be informational and timely, and to aid further planning activities.

The document is not a rigid template for all future great lakes research. In most cases the report chapters identify research that is feasible, and even desirable to undertake, but the harder tasks of setting strict priorities and estimating costs are not included. The body of this report is aimed at the large community of scientists engaged in great lakes research, in order to encourage a unified and coherent development of priorities.

The dominant themes in future great lakes research which emerged from the workshop are expressed in the four summary issue chapters (3 to 6). The chapters are a blend of ideas drawn from discipline group discussions, background papers, and draft revisions. The interactive process of report preparation makes assigning individual authorship difficult, but the issue chapters were written principally by Issue Group Chairs (D'Elia, Knoechel, Melack, Powell, Werner: Appendix C); Chapter 6 is a composite of reports from Food Web and Comparison Studies groups. Discipline Reports were written by group rapporteurs (Appendix C).

2. SUMMARY RECOMMENDATIONS

GREAT LAKES RESEARCH

Large lakes are enduring features of the earth, even during epochs of geological stasis. They hold much of the world's liquid fresh water, from cold, ice-clad basins in the Canadian Arctic and Siberia to the warm chemically stratified lakes of the East African Rift. Individual basins range in age from less than 10,000 to over 60,000,000 years.

Despite their global distribution and significance as aqueous reservoirs, great lakes have received little attention from the scientific community. The lakes require oceanographic techniques, but many are landlocked basins which the research fleet cannot enter. Where access is possible, multi-disciplinary challenges have slowed progress. Oceanographers encounter diverse water chemistries and biota alien to their experience, and limnologists encounter classes of physical phenomena, and interactions between physical and biological processes, that do not occur in small lakes. These obstacles have slowed for too long the investigation of environments which offer knowledge about important ecological and evolutionary processes.

Great lakes are basins large enough to respond to all the major physical forces that drive the atmosphere and oceans, to an extent that ecological phenomena cannot be studied with reference to biology alone. Hydrographic segregation of inshore and offshore regions promotes the divergent development of separate biological communities from a common species pool. The lakes typically have greater faunal species richness than individual small lakes, in part because they present more heterogeneous habitats. Great lakes, moreover, include the only freshwater environments with deep benthic fish communities.

The antiquity and isolation of some great lakes have permitted substantial species evolution among their faunas. The sediments of these lakes hold not only the fossil records of lacustrine evolution, but also the records of terrestrial vegetation and regional climate. High sedimentation rates and excellent preservation of stratigraphy offer a paleoecological record spanning the Tertiary and Quaternary with potential resolutions of seasons to decades. No long cores have ever been raised from these lakes, even though some of the most promising sites would help resolve the climate and conditions during man's own evolution.

At present, the great lakes of the world are experiencing novel and extensive perturbations. An exotic piscivore introduced to Lake Victoria, for instance, is forcing extinctions among the endemic community of cichlid fish. Petroleum explorations in the relict Lakes Tanganyika and Malawi may put at risk the protein supply of several million lakeshore people. Conditions are poised for experiments in massive species extinctions, but the baseline conditions are barely known to science.

Great lakes are unarguably great ecosystem laboratories for the experiments of nature and man. The basins differ in nutrient income, hydrologic flushing, morphometry, age, latitude, circulation patterns, and ionic composition. They experience different magnitudes of human influence. Freshwater biological communities are far less diverse phylogenetically than their marine counterparts, even in relict lakes. They invite detailed analyses of food webs, species interactions, and community ecology. The progress of species invasions can be charted within the lakes, and the reasons for species extinction, or evolution, may be understood.

Finally, the rise of new technologies has made research problems in great lakes tractable as never before. The present state of remote sensing techniques from satellites and aircraft permits resolution of physical structures that match with biological processes of great interest. It also offers the novel chance to survey the offshore biomass and productivities of great lakes world-wide to examine the roles of latitude and climate in determining these aspects. Simultaneously, the advent of new molecular technologies makes possible better identifications of stocks and genetic heterogeneity among great lakes species. These are new tools to probe the phenomenon of biological species evolution in basins where fossil histories are available for reference.

RESEARCH INITIATIVES

Progress in basic science relies on breakthroughs and insights, which are intrinsically difficult to manage or initiate. Nonetheless, it is possible to identify general issues and inquiries that are fundamental and prerequisite to major lines of research. In most cases the technical feasibility of a project exceeds the ability of individuals or single institutions, so that progress can occur only through the concerted efforts and encouragement of a large scientific community. In other cases, opportunities arise by invention of tools or approaches that make important but previously intractable problems suddenly tractable.

The present state of scientific capabilites dictates that priority of attention and resources can be directed at five major initiatives in great lakes research. The goals are attainable within the next 10 years.

Raising Long Cores from One or More Ancient Lakes

The technology for this endeavor has already been developed in the Ocean Science Deep Drilling Project, but the target lakes of greatest priority are in Africa and are landlocked. A feasibility study and advisory committees must be established to guide the site selection and disposition of material.

Mass and Material Budgets for Major Biogeochemical Elements

Complete input-output budgets are presently lacking for all biologically important elements in all the great lakes of the world. Progress in biogeochemical and ecological investigations will be hindered until some of these fundamental data are produced. The elements of greatest interest are carbon, nitrogen, phosphorus, silicon, iron, and manganese. Because the lakes are enclosed basins, these budgets are attainable, and they should

be attempted for several arctic, temperate, and tropical sites. Residence times for these elements are probably longer than those characteristic of small lakes, but less than characteristic times in the ocean. Great lakes present the only opportunities in this mesoscale time range to examine biogeochemical properties and to forge a link between lake and ocean studies.

Mesoscale Physical Features and Associated Biological Phenomena

The existence of an enduring coastal zone is a feature that distinguishes large lakes from small ones. The magnitude of this phenomenon may be dependent on latitude, owing to the influence of the Coriolis effect. Transport between nearshore and offshore regions influences productivity, sediment distribution, and development of biological communities. The physical features involved are upwellings, thermal fronts, plumes, jets, and other structures also found in the coastal ocean. Closed basin circulation and oscillations produce novel manifestations of these phenomena in great lakes. Furthermore, climate and morphometry control the physical circulation and flushing times of the basins, with associated effects on rates of biological processes.

Organization and Evolution of Biological Communities

Some taxa of fish and benthos have radiated into new species in great lakes environments, whereas most plankton have not. Most plankton species have broad regional or cosmopolitan distributions, but their dominance varies among lakes owing to ecological interactions. Great lakes permit study of how new species arise and how individual communities are crafted from larger species pools. The roles of resource availability and biotic interactions in community structure need careful attention. New molecular technologies should be exploited to decipher the genetic bases of evolutionary processes in nature.

Trophic Dynamics and Productivity

Studies of carbon flow in great lake ecosystems should emphasize rates and processes, using common methodologies, so that comparison studies among ecosystems can be initiated. Investigations of the mechanisms that control these fluxes across scales of lake basin size and latitude, and with marine environments, are particularly important. The studies must address microbial pathways and ecological transfer efficiencies to upper trophic levels, because ecosystems of different age and spatial complexity may differ in trophic structure and efficiency.

INSTITUTIONAL ARRANGEMENTS AND FACILITIES

Great lakes research is handicapped by lack of equipment, instrumentation, and research platforms. Efforts to assemble a pool of modern deployable instruments must begin at once. In order to assure acquisition of standard and compatible instrumentation, some degree of coordinated and advised authority is necessary. Several institutional arrangements, under one or more administrative umbrellas, are needed to accomplish these goals. Otherwise the efforts will fail, not because they are unimportant, but because no individual can marshal the resources to accomplish the scientific goals. The most effective motives for coordination are specific

experimental goals around which successive, finite programs can evolve. The administrative structures to support these efforts should reside at academic institutions, where the joint emphases on research, teaching, and synthesis match the fundamental goal of improved understanding.

Consortium for Great Lakes Instrumentation

A centralized authority is needed to acquire instrumentation and apportion it for studies of great lakes. High priority is assigned by all users to automated and standardized data acquisition. Cooperative efforts among many investigators will be required to obtain the instruments, and some engineering and technical expertise will be required for maintenance and service. The instrumentation would best be housed at an institution bordering the Laurentian Great Lakes, within easy access of an air cargo shipping point. Acquisition, use, and scheduling of this multi-user equipment should be under the direction of a rotating user group with representatives from the U.S. and Canada.

Great Lakes Data Center

An organized archival facility for limnological data should be established. The archival facility should be accompanied by a small grants program to maintain a low level of support for continuing analyses of archived data. A review committee and a professional charged with curatorial duties will be needed to select old and new data sets appropriate for archiving. It would be most satisfactory if this facility were associated with a satellite dish and computing capabilities devoted to the acquisition of raw remote sensed information relevant to great lakes processes. The archival facility should be an associated service unit of an institution committed to basic research in great lakes. Existing institutional computing facilities and data communication networks should be employed.

International Great Lakes Research Unit

The International Association for Theoretical and Applied Limnology (SIL) has recently promoted coordinated programs of research in developing countries. Great lakes of considerable scientific interest exist in some of these countries. A central office is needed to facilitate research, mobilize resources, and coordinate activities. This office could increase the exposure of indigenous scientists in developing countries to outside expertise. Liaisons are encouraged among SIL, ASLO (American Society of Limnology and Oceanography), and IAGLR (International Association for Great Lakes Research) for this goal.

Long-Term Data Collection

Reference sampling stations and reference measurements must be established for the Laurentian Great Lakes and for other great lakes where access is feasible. Reliable long-term data for large lakes are of great ecological value, but they are in short supply. Ongoing and planned monitoring programs by federal, state, and provincial agencies should be coordinated and guided by the needs for scientific knowledge. By adopting an ecosystem perspective on the great lakes it should prove possible to design data collections consistent with the missions of EPA, NOAA, and other agencies that simultaneously address present gaps in knowledge.

Coordinated efforts toward this goal would promote efficient use of resources and scientific talent.

Planning Activities

Standardizing techniques and selecting reference stations for study will require technical discussions and debate. One future workshop should be convened with the charge to produce recommendations on these issues. In addition, a symposium is desirable on emerging technologies applicable to limnology.

Most importantly, representatives of agencies involved with scientific issues in great lakes must begin a dialogue aimed at promoting an integrated understanding of the lakes. Resources for environmental research must be used in a valid and scientifically defensible way. Monies spent on administrative support structures will be wasted unless tangible scientific progress results. This is now the time to undertake assessments of the status of support for great lakes research and its effectiveness. Efforts to meet the scientific challenges identified in this report can begin immediately.

3. SCALE DEPENDENT PROCESSES AND INFLUENCES

PROBLEM DEFINITION

Every physical or biological process exhibits characteristic space and time scales in nature. In aquatic systems the processes range from rapid, molecular reactions to phenomena induced by the rotation of the earth or by species evolution. Because of their immense size and age, the great lakes of the world exhibit the full spectrum of freshwater phenomena. Many of the processes which occur in these large bodies of water cannot occur in smaller or younger lakes.

It is not possible to comprehend the relevant physics and biology of great lakes by reference only to analog studies on small lakes. Neither is the world ocean an adequate analog, because great lakes are bounded basins inhabited by freshwater organisms. Investigations in these basins directed at both short and long time scales, and at small, medium, and large spatial scales, would answer longstanding and important questions in limnology, oceanography, and ecology. The great sizes and ages of these lakes permit investigations of how processes acting at one spatial or temporal scale influence events at another.

RESEARCH GOALS

Although studies of either the physics or biology of large lakes offer considerable interest individually, special demands exist for coupled investigations. In many cases, neglect of the physics can compromise conclusions based solely on biology, and vice versa. Our goal is to promote a judicious mix of field measurements, remote sensing, and statistical and mathematical analyses of extant data. Modeling of processes and their interactions is important because models are diagnostic tools whereby system behavior may be better understood and data may be better interpreted. Data collection and theory must develop in parallel.

EMERGING RESEARCH OPPORTUNITIES

Six characteristics of the world's great lakes are noteworthy for the scientific opportunities that they provide. Three of these characteristics are related to the sizes and ages of the lakes, two involve the influence of associated watersheds, and the last concerns the wide latitudinal distribution of great lakes globally.

Great lakes are large enough to respond to all the basic physical forcing mechanisms that affect the oceans, but they are small enough to be manageable logistically and synoptically. The lakes are large enough to be influenced by the Coriolis effect, which produces many, if not most, of the hydrodynamic complexities found in the atmosphere and ocean.

The lakes exhibit an array of mesoscale effects which arise by interaction of small scale ("micro") processes, like turbulence, and large scale processes, like basin-wide circulation. Mesoscale phenomena may be more easily studied in large lakes than in the ocean, evidenced by the pioneering air-sea interaction studies performed in the Laurentian Great Lakes of North America.

Great lakes of the world differ considerably in age. They range from the great relict Lake Baikal which dates at least to the early Tertiary, 60 million years, to the great relict lakes of Africa, Asia, and Europe, and finally to great lakes of late glacial origin, such as Great Bear Lake in the Canadian Arctic, less than 7,000 years old. These are the best environments in which to ask paleolimnological questions about the evolution and progression of lake systems. Their sediments also contain a rich history of the events in their basins and watersheds during the span of time covering the evolution of many modern species, including man. Great lakes, moreover, are enduring, perennial features of the earth's geological history. The countless small glacial lakes of the Quaternary are transient results of Pleistocene glaciations, but great lakes of tectonic origin have doubtless existed throughout geological time. The fossil sediments of these ancient lakes can extend the age scale even further.

Lakes are enclosed by their basins. It is possible to sample the same water and the same populations repeatedly within the basin, month after month or year after year. This opportunity is not duplicated in the ocean, where sampled water has typically been "processed" elsewhere. Studies of lake ecosystems can thus have a unique coherence and integrity. They offer the opportunity to construct and refine models of chemical budgets or trophic dynamics across a range of flushing times, hydrographic regimes, and climatic conditions.

In great lakes direct interaction between watershed and pelagic waters is probably reduced in comparison with small lakes, and, correspondingly, airshed effects are more apparent. Great lakes are good global monitors for natural and synthetic volatile compounds because budget building is possible. Although local episodic interactions from inflowing rivers can be important at small spatial scales and brief time scales, the effects diminish when measured at the annual or basin-wide scale. In any year, for instance, the contribution of phosphorus supplied to the pelagic regions of great lakes from watershed sources may be small compared to the total mass of P in the lake. This means that the lakes have genuine offshore regimes with their own nutrient dynamics.

Large lakes are found from equatorial to polar regions. This latitudinal distribution leads to large differences in climatic and geological circumstances which provide natural experiments on the effects of these circumstances on the structure and function of communities and ecosystems.

RECOMMENDED RESEARCH INITIATIVES

Short Time Scales: Critical Timing of Events of Short Duration

Events of short duration which immediately precede, accompany, or closely follow the period of least stable stratification can be crucial to entire annual progressions in lakes. For example, high runoff at precisely the time of turnover could distribute an important nutrient throughout a lake basin. An intense storm during a period of low stability could accomplish complete vertical overturn in a lake that might otherwise remain incompletely mixed. Such events strongly influence both vertical and horizontal thermal structure, and they affect phytoplankton biomass, productivity, and community composition, but little is known about the mechanisms of interaction.

The development of both vertical thermal structure and horizontal temperature variation needs thorough investigation. The details of formation of epilimnion, thermocline, and hypolimnion may hinge on the advance of a thermal front toward mid-lake. Most important is the response of phytoplankton to this progression, particularly the timing of algal blooms and their location relative to the thermal front. This study will involve detailed time series data collection at one or a few stations, a series of whole lake transects, and remote sensing of the entire lake. The resources of several collaborating institutions and two or more vessels will be necessary. The measurements should be repeated for several years in order to sample the interannual variability at the critical period.

Because little is known about water mass motion in winter, the measurement program should include attention to conditions before the "minimum stability" period. Better measurements are needed for the adiabatic temperature gradient than have commonly been recorded in the past.

Long Time Scales: Studies of Interannual Variability

Many important and interesting research questions require investigations over more than one or two years. When the questions involve events spanning many decades to centuries or millenia, the paleolimnological record is the only appropriate medium for study. The paleo-record, unfortunately, is selective and descriptive only; it provides no proof of process or interaction. More effort is needed to intercalibrate paleolimnological records with long-term neolimnological data in order to understand the values and limitations of the records. Individual years may be usual or exceptional in terms of limnological events, but the exceptions and their importance are impossible to recognize when data are rare.

Several long-term data collection sites should be established on carefully chosen lakes to permit inquiries about events on time scales of years to decades. Consistent sampling of a limited number of parameters will prove more valuable for this work than attempts to sample many parameters for short periods. The guidelines for analyses and distribution of data should follow the prescriptions outlined in Chapter 4: Chemical Fluxes and Biogeochemistry. The criteria for selecting such sites should include the condition that good paleolimnological records be obtainable from the basins. Because of the extreme paucity of existing long-term consistent records, any which do exist should be subjected to analysis with highest priority. Such efforts will yield designs for future studies that offer the most reward.

The long-term studies must be designed to answer fundamental questions about interannual variability in lakes. First, they must determine whether large and small lakes are equally sensitive to climatic events and climatic change. Also at issue is the relative susceptibility of tropical and temperate lakes to catastrophic perturbation. Temperate lakes face strong seasonal signals of photoperiod and surface temperature, whereas in tropical lakes these features are more constant. Temperate and tropical lakes may respond differently to natural or man-made aberrations, and the effects of a perturbation may propagate differently in each system.

A central, unresolved issue is whether large lakes are more or less variable temporally than are small lakes. Some workers believe that large lakes have physical and biotic inertia that limits their interannual changes in comparison to small lakes. Opposing this is considerable evidence from large lakes, estuaries, and the ocean showing more variability at large spatial scales than at small ones. How the evident large spatial variability might translate into low temporal variability is a very fundamental question about scale dependency in general. It may be that a critical size scale exists, governed by physical phenomena and biological processes, above which larger basins show greater variability, and below which smaller basins show greater variability. If such a scale does exist, it may reflect physical constraints like the Rossby radius of deformation, a loose dynamical boundary between the coastal and mid-lake regions.

Small Spatial Scales: Formation, Progression, and Decay of Small Scale Vertical Interfaces

Sharp interfaces between water masses of different densities are common, evidenced by an extensive literature on thermal microstructure. Several vertical structures can form, evolve, and decay during a single season. The structures can occur at the surface, at the sediment-water interface, or as lenses in midwater. Extreme gradients in biomass, productivity, and species composition often develop across these interfaces. Little is known of the mechanisms for formation, progression, and erosion of these features, and even less of their persistence and horizontal extent. There is evidence from small lakes that vertical microstructures contribute to whole-lake processes of primary productivity, nutrient transport, and seasonal succession of species.

The coupling of physical and biological processes at these interfaces can produce a suite of complex ecological phenomena. Near-surface interfaces may be sites of strong photoinhibition, with consequent importance to rates of overall lake productivity. When the interfaces are stably stratified they can exist longer than neutrally buoyant, unstable lenses. If they persist, intense predation or competition for nutrients might occur within such regions at rates far greater than those of the water column on average. The proximate mechanisms might be through influences on aggregation behavior of zooplankton, or through effects on sediment-pelagic coupling of nutrient transport.

Investigations of these spatial relations must always proceed in reference to the temporal scales of variability identified in the preceding initiatives. In any one year many lenses may form as a result of high inputs of energy or momentum owing to slight changes in the local climatic regime. In another year climatic events might allow only a few interfaces. Interannual variability must consequently be assessed before any general conclusions are drawn.

The small vertical scale of these phenomena demands fine spatial resolution for sampling. Moreover, some interfaces may be short-lived, and so sampling must be frequent. Some attempts to look at these phenomena in the ocean have been tried, but over much shorter periods than we envision.

Nonetheless, the oceanic examples provide useful lessons in data management and analysis.

Some small interfacial phenomena may be linked with much larger scale effects. Surface cooling by evaporation, for example, could trigger intense vertical motions in an initially stable interface. Such free or forced convection could rapidly overturn a whole lake. A similar mechanism may have caused the tragic 1986 event at Lake Nyos, Cameroon. The critical timing of such events could be extremely important, as indicated in the initiative on short time scales.

Mesoscale Phenomena: Nearshore-Offshore Transport

The existence of a separate coastal zone is a feature that distinguishes large lakes from small ones. The boundary between coastal and midlake regions may be topographic, like a "continental" shelf, or dynamical, like a cross-shelf distance equal to the internal Rossby radius of deformation. Transport between nearshore and offshore regions may involve transfer of dissolved nutrients, organisms, or fluid directly, or it may involve the transfer of energy or momentum, through lateral friction. The general transport process consists of a series of individual episodes, and each one may contribute to algal blooms, deep chlorophyll maxima, productivity, and sediment transport. Until now, the contributions have been investigated only qualitatively and anecdotally. Of the initiatives proposed for study in the great lakes of the world, this one may be most important and deserves highest priority.

The goal of this investigation should be a complete quantitative description and model of nearshore-offshore transport processes with reference to heat, nutrients, and particulates. Integrated studies should focus on restricted spatial regions where past experience and remote sensing have demonstrated that processes of interest occur almost every year. Several events are of special interest because they seem to have particularly strong effects.

Upwelling episodes bring nutrient-rich water to the euphotic zone, as they do in the coastal ocean. Lake and ocean upwelling episodes are likely different, however, owing to the enclosed basins of lakes. Upwelling may end much more abruptly in lakes than in the sea. Upwelling water is not renewed in the same ways in each system and lake upwelling events are more short-lived. This unique behavior in lakes introduces a characteristic time scale, the "efflux time," which does not exist in the ocean.

Thermal fronts, also called thermal bars, promote different patterns of circulation from one side of the front to the other. Mixing similarly varies across the fronts, and is intense at the frontal region.

Squirts, jets, filaments, and plumes are high velocity events which appear to be common, if not permanent features of the coastal zone based on satellite images of large lakes. The overall rate of nearshore-offshore transport is the ensemble of these small scale events averaged over long times. The relationship of these qualitative features to the magnitude of transport has not yet been elucidated quantitatively. These phenomena are

so general and important in all coastal regions that investigations should complement companion studies in the coastal ocean, where analogous structures exist.

Sediment resuspensions contribute to sediment distributions in ways understood only fragmentarily. Offshore transport events in the early spring, for instance, seem closely associated with a particularly active region of sediment deposition in Lake Michigan near Benton Harbor, along the southeast shore of the lake.

A coordinated study directed at these phenomena will involve an observational program based on current meters, drogues, and CTD sections. Sediment collections and, at the very least, detailed chlorophyll distributions will be needed as well. Focus on one single spatial region at first will allow the necessary intensive measurements, which should be coordinated closely with remote sensing information. The mathematical and numerical models developed to interpret these mesoscale structures will certainly need to incorporate non-linear terms in the equations of motion.

Large Spatial Scale: Comparisons of Great Lakes with Landlocked Seas

Despite their sizes, the world's great lakes are generally smaller than most of the enclosed and semi-enclosed seas on earth. Just as comparisons can be made between large and small lakes, similar comparisons can be made between large lakes and the larger landlocked seas. Almost all of the physical forcing functions are identical, except the effects of salinity. Although species differ, they share similar responses to light, nutrients, temperature, and predation risk. The general processes which govern distributions of phytoplankton in space and time should be similar in these systems. If great lakes and small seas should demonstrate consistent dissimilarities, however, the differences would be of fundamental interest to both limnologists and oceanographers.

This initiative must proceed in two phases. The first step is to identify satisfactory study areas. Remote sensing and numerical models may help uncover regions where similar patterns are expected consistently. Satellite imagery from Lake Michigan and the Baltic Sea, for instance, shows remarkable similarities between the two coastal zones and the pelagic regions. After the sites are identified, field programs can be initiated. Drogues, current meters, CTD (conductivity, temperature, depth) and chlorophyll sections, and sediment collectors should be employed to describe the details of evolving patterns in both bodies of water. The studies will enhance cross-disciplinary discussions between limnologists and oceanographers. Oceanographers have long recognized the importance of physical constraints on biological processes; limnologists, on the other hand, have developed a wider appreciation of the diversity of biological phenomena. Each discipline can benefit from the collaboration. Such comparison studies will require a degree of international cooperation and consent. Institutional structures to facilitate the work will be necessary (see Institutional Arrangements and Facilities).

Theoretical Models

Few theoretical models of aquatic systems treat both spatial and temporal aspects of the ecological phenomena under investigation. Physical processes dominate the transport of organisms, nutrients, sediments, and other properties in water bodies, and they sometimes even dominate the rates of change of ecological properties of interest. Disregard for physical transport in ecological modeling efforts traces to the considerable difficulty of incorporating the features. We strongly encourage efforts to include spatial and temporal variability in future models of the world's great lakes.

INSTITUTIONAL ARRANGEMENTS AND FACILITIES

The goals of the initiatives proposed above are predicated on the development of facilities and institutions, as well as acquisition of equipment, over the next ten years. This time horizon is appropriate to our present ability to identify research challenges, and also to the developments required. Most of the following recommendations concern the Laurentian Great Lakes of North America, because they present viable research opportunities and the most feasible logistics. However, one of the institutional arrangements is devoted to lake studies outside the developed countries.

Facilities

A large, stable, year-round vessel, commissioned solely for Great Lakes research, is desperately needed. The RV Laurentian is too small to work in seas approaching two meters. It consequently is an unreliable platform from which to study events at overturn. Perhaps a larger ship from the UNOLS fleet can be devoted to this specialized assignment. Several speedy "hovercraft" type vessels are needed as well for rapid synoptic surveys.

The research community needs rapid access to remote sensed data. The largest obstacle to utilization of potentially valuable satellite information is the unacceptably long delay between acquisition of data and their availability to researchers. At least one plane instrumented with spectral capabilities for dye tracing would be extremely useful. The sensing system should be expandable to additional spectral bands. The capability to collect data during the times when in situ aquatic measurements are being performed would be important.

Equipment

Several types of equipment are in extremely short supply within the Great Lakes community. Efforts should be made to acquire the following instruments and to hold them in a communal pool for research use, in much the same way that research vessel time is apportioned.

a) Microstructure profilers for measuring temperature, conductivity, and velocity.
b) Moored, in situ fluorometers
c) At least six LORAN tracked drogues with skirts that can be adjusted to follow water at given depths.
d) Moored acoustic instruments, including upward-looking SONAR, that either transmit to satellites or are cabled to shore.

e) Multi-spectral scanners that extend to the infra-red to sense algal pigments, including chlorophyll, pheopigments, and accessory pigments.

Three organizational arrangements are proposed to facilitate the efforts we have outlined for the next decade. The arrangements are necessary because substantial endeavors in the future will involve many investigators from several institutions, probably not all from the U.S. Multidisciplinary constructs are needed, and disciplines like astronomy, high energy physics, oceanography, and space science may provide the best models.

Data Center

Few researchers publish all or even most of the data they collect. In many cases the information is thus fragmentary, tentative, and of marginal use to anyone. There are nonetheless particular types of data, especially those collected with standardized shipboard profilers, that have universal applicability. An organized archival facility for limnological data would aid the task of bringing important, buried information to light. Scientists often face difficulties when trying to garner support to analyze existing data, and that has contributed to the unfortunate practice of unintended burial of data. The archival facility should be accompanied by a small grants program to maintain a low level of support for continuing analyses of archived data. Funds should permit individual investigators to conduct computer assisted analyses of data that are subsequently assigned to the public domain.

Consortium for Laurentian Great Lakes Instrumentation

High priority is assigned by all users to automated and standardized data acquisition. Cooperative efforts will be required to obtain the instruments, and technical expertise will be required for maintenance and service. The instrumentation should be housed at an institution bordering the Laurentian Great Lakes, within easy access of an air cargo shipping point. Selection, use, and scheduling of the multi-user equipment should be under the direction of a rotating user group with representatives from the U.S. and Canada.

International Great Lakes Research Unit

The International Association for Theoretical and Applied Limnology (SIL) has recently promoted coordinated programs to study limnology in developing countries. The SIL also established a Working Group on African Great Lakes in which scientists are coordinating research and guidance of resource exploitation in these waters. Many great and relict lakes exist in Asia, Africa, and Central and South America which are of considerable scientific interest. Particularly inviting are comparative studies between the Laurentian Great Lakes and these remote great lakes. We endorse efforts to promote liaisons among SIL, ASLO, and IAGLR for the purpose of facilitating such studies. A central office for inquiries and coordination in the U.S. or Canada would be most helpful. The UNESCO-sponsored International Centre for Theoretical Physics in Trieste, important to physical scientists in developing countries, provides a successful model for such endeavors.

4. CHEMICAL FLUXES AND BIOGEOCHEMISTRY

PROBLEM DEFINITION

Inquiries about chemical fluxes, biogeochemistry, and nutrient cycles are of special importance in both scientific and management contexts. In most cases, scientific understanding and management capabilities are inextricably linked. If the pathways and processes by which materials move through ecosystems are not understood, it is impossible to make learned judgements about the risks of particular perturbations or resource exploitations. Past research into biogeochemical phenomena has been hampered by the traditional separation of the disciplines of chemistry, biology, and physics. Proper understanding of the fluxes and processes requires a coordinated interdisciplinary approach. Complex nutrient cycles such as that of phosphorus, for instance, involve physical advection and stratification, chemical sorption and desorption, and biological uptake and regeneration. An interdisciplinary approach is critical for interrogating nutrient element distribution and partitioning. The same is true for the cycles of other key elements and exotic substances.

Development of diagnostic models of the biogeochemical cycles of carbon and the major nutrients is a central goal that illustrates the underlying linkage between science and management. The models achieve several aims simultaneously; they synthesize information about processes, focus research efforts where needed, and provide consistent system descriptions. When combined with expert judgement, accurate models can improve predictions of ecosystem responses to managed or natural perturbations. Resource management necessarily benefits from scientific progress and improved understanding of ecosystem structure and function.

Large lakes exhibit many features of inherent scientific interest and pose many management issues of an economic and public health nature. An ecosystem context for inquiries about these lakes provides a plausible framework for the stewardship of water quality and fisheries resources. Information about causal relationships is generally lacking and management decisions have been guided by extrapolated statistical models. Ecology as a science suffers the inability to predict system responses, and ecological understanding of great lakes is no more advanced than that of the discipline as a whole. Long overlooked, however, is that great lakes offer unique advantages as ecological systems for study. For example, average depths vary from >1,000 m in the great relict lakes to less than the depth of normal thermal stratification in others. Nutrient inputs and stocks of biomass differ. Not only can the lakes be compared and contrasted with each other, but they provide a range of characteristics exemplifying water bodies from the size of small ponds to that of oceans.

RESEARCH GOALS

Biogeochemical inquiries must emphasize the development of mass balance budgets for the elements of interest. These can be as simple as box models which characterize pool sizes and fluxes into and out of the system. Such biogeochemical budgets are generally lacking for all the great lakes. Even for the Laurentian Great Lakes, only the budgets of ^{210}Pb, Pu, and

^{137}Cs are reasonably well known. Formulation of elemental budgets should be the earliest goal of future research in this area. These efforts will identify the most significant gaps in knowledge and will encourage more detailed budgets and models. Simple budgets almost certainly will uncover important contrasts among lakes, and will help identify material sources and sinks that function on a global scale in freshwater ecosystems. Subsequent advances will be the development of sophisticated process models, and ultimately even predictive ecological models. All this hinges at the outset, however, on reliable knowledge of mass balance and materials flux.

EMERGING RESEARCH OPPORTUNITIES

Exchanges across boundaries or interfaces are often the rate-determining steps in biogeochemical cycles. Chemical constituents move from sources to sinks by cycling pathways that are sometimes simple and sometimes complex. Changes in oxidation state, chemical form, or mobility are determined by diffusion, advection, and reactions at the interfaces between one chemical pool and another. The major interfaces relevant to biogeochemical cycles are common to aquatic systems of all sizes, but studies in large lakes have particular advantages with regard to large scale phenomena. Interactions at individual boundaries can be isolated spatially, and comprehensive research efforts remain logistically feasible. The relevant interfaces are:

a) atmosphere-lake
b) particle-water or particle-solute (including biological assimilation)
c) sediment-water
d) aquifer-lake
e) land-water

Studies of the processes active at these boundaries should be integrated into quantitative mass budgets for the entire system. Such referencing yields an assessment of the relative importance of individual fluxes and a refined understanding of major chemical pathways.

RECOMMENDED RESEARCH INITIATIVES

Baseline Reference Stations

Long-term data are vital for identifying periodic and aperiodic natural phenomena as well as the cumulative effects of anthropogenic alterations. A few permanent reference stations should be established throughout the Laurentian Great Lakes. Sampling frequency should be appropriate to the statistical requirements of time-series analysis for annual and seasonal changes. The best, current analytical procedures should be used for most measurements, which means that procedures will change as methods evolve. However, because long-term comparability and consistency are also important, selected parameters should also be determined analytically by "reference" procedures that do not change. Data should be posted on computer-linked data services for all interested parties, but also reviewed continuously by scientists trained to recognize unusual events and to evaluate patterns in time and space.

The monomictic to dimictic nature of the Laurentian Great Lakes makes investigations of long-term trends particularly inviting in those basins. Concentrations of chemicals become essentially constant through the water column in winter, as water and suspended bottom sediments become well mixed. By sampling only a few stations in each lake prior to stratification, reference chemical pool sizes can be established accurately. Sampling at the start of the "limnological year" in late winter will provide data at a time when the influences of biological processes on chemical properties are at a minimum. This important annual "resetting" of the Laurentian Great Lakes provides an opportunity to census lake chemical contents accurately and economically. If it proves to be a fruitful approach it can be extended to many other basins.

Establishment of sampling stations should take into consideration accessibility to major research institutions in order to minimize cost and maximize effective use. Selection of analytical methods and quality assurance should follow guidelines developed by high quality programs like GEOSECS. Scientific concern over analytical procedures adopted as standard by some federal agencies requires that caution be exercised in the selection process and that historical data be viewed with necessary skepticism.

<u>Carbon Biogeochemistry</u>

No adequate carbon budgets presently exist for any great lake. Past investigations have been fragmentary and short-term, and neither integrative nor synoptic. Thus it is not possible to assess total budgets for the lakes, or to examine variations in the carbon cycle within or between lakes.

The carbon cycle should be the entree to the study of biogeochemistry in great lakes. It shares commonality with many other cycles that are linked with carbon, as well as with scientific inquiries about productivity, biomass, and trophic transfer efficiencies. The intellectual approaches and the methods for storage and dissemination of data that are developed for the study of carbon budgets will influence the developments of other elemental budgets. The principal topics of inquiry necessary at the outset to achieve this goal are:

a) primary productivity (carbon fixation by phytoplankton)
b) carbon remineralization and bacterial production
c) carbon sedimentation and burial
d) diagenesis and remineralization of sedimentary carbon.

These categories generalize the carbon budget into a small number of major pools and fluxes, an appropriate first step. The processes responsible for carbon cycling are complex and diverse, involving transfers among many trophic levels. Further development of the details and their biological consequences are considered in Chapter 6 (Food webs, community structure, and trophic relations).

<u>Nitrogen Biogeochemistry</u>

Because nitrogen has not been considered a growth-limiting nutrient for phytoplankton in most lakes, it has been overlooked as an important diagnostic tool of ecosystem processes. The nitrogen cycle is mediated

primarily by biological processes. This characteristic distinguishes it from the cycles of both phosphorus and silicon which prominently feature both biological and chemical processes. Nitrogen thus provides a tool for interrogating certain biological processes in a way unlike the other elements.

As the first step, budgets should be built to establish whether large lakes are sources or sinks for atmospheric nitrogen. Whether nitrogen fixation exceeds denitrification or not needs evaluation, as does how these balances compare with measurements from estuarine and oceanic environments.

Secondly, cycling of bound nitrogen in the water column, and between epilimnion, hypolimnion, and sediments deserves careful evaluation. The time scales of cycling phenomena need particular attention. The upper Laurentian Great Lakes, in particular, differ from oceanic environments in the high levels of nitrate relative to phosphate found in the water. Mass balance studies are the best way to identify the reasons for this fundamental and striking difference.

Finally, the airshed-lake interface provides an important research opportunity. Relatively little is known about inputs of nitrogen to aquatic systems through precipitation, or whether such inputs are now increasing. The offshore waters of great lakes provide an excellent natural laboratory for measuring the fluxes.

Phosphorus Biogeochemistry

The pivotal role that is played by P in eutrophication of lakes and regulation of biomass makes it a priority element for mass balance and process investigations. Phosphorus has received more investigative attention within the Laurentian Great Lakes than any other nutrient element, but comprehensive and quantitative analyses of its biogeochemistry are not yet realized.

The phosphorus cycle differs between great lakes with oxic hypolimnia and those with permanent or seasonal hypolimnetic anoxia. Dissolved phosphorus is often released to the water under anoxic conditions, and the nutrient can have a strong fertilizing effect when mixed into the surface waters. Even in oligotrophic great lakes, however, the hypolimnion and sediments probably remain the dominant annual source of P for phytoplankton in the lake, through transport during particle resuspension. Sorption and release of P to and from suspended particles buffer concentrations of P by maintaining dissolved P at low levels, but providing a steady supply to phytoplankton through equilibrium dissociation reactions. Resuspension of particles during overturn is an extremely important source of P to the photic zone. Differences in mixing conditions between years and basins may have striking consequences for productivity patterns. In temperate lakes, the amount of particle-bound P left and recycled in the epilimnion at the onset of stratification is likely a major factor controlling summer primary production in photic zones. After stratification, primary production in the euphotic zone relies mainly on biological recycling. The relative importance of several uptake and release processes are not fully known, and they deserve careful integrated study:

a) excretion by micro- and macro-invertebrates
b) autolysis of dying algae
c) degradation of organic P by bacteria
d) algal uptake versus bacterial uptake.

Present understanding of chemical and biological mechanisms affecting the P cycle in water and sediments is clouded by the unknown diversity of chemical forms of P and by the tendency of P to adsorb to particles. This sorption makes it difficult to study rate processes involving dissolved P and particles, such as mineralization in sediments. Progress will require considerable analytical skill and ingenuity.

Silicon Biogeochemistry

The biogeochemistry of Si contrasts both with P, which has a much more complex nutrient cycle and often more rapid turnover, and with N, which is a constituent of all biota. The cycle of Si is less complex than other nutrients because only insignificant quantities of mass are assimilated by secondary producers and transferred through the food chain. Consequently, Si provides a tool to focus analysis on specific ecosystem phenomena, particularly among primary producers.

The silicon cycle in lakes involves biological assimilation of silicic acid primarily by diatoms and chrysophytes, formation of biogenic silica, death of siliceous organisms, and chemical dissolution of biogenic silica. Although weathering of crystalline silica from the lithosphere ultimately provides the silicic acid, it is the formation and dissolution of biogenic silica that regulates concentrations of silicic acid in lake waters. The relationships between biogenic production and geochemical processes are tightly linked, compared with other nutrients, because of the following characteristics of the silicon cycle:

a) no food chain transfer to upper trophic levels
b) no chemical transformation except dissolution before permanent burial

These features make budget-building exercises conceptually simple for silicon, and simultaneously make it an excellent prospect for comparisons among ecosystems.

Iron and Manganese Biogeochemistry

Iron and manganese are critical to biological productivity and to geochemical control of other nutrient cycles, particularly that of P. Concentrations of these trace metals are very low in oxic epilimnia, and there are reports of co-limitation of algae by P and Mn in oligotrophic Lake Superior. The role of these trace elements deserves study across the wide spectrum of chemical environments in large lakes, from dilute soft-water systems to hypersaline ones. Such a spectrum is obviously not available in marine habitats, and the global geochemical role of these elements may be incompletely understood because of it. Unlike many of the initiatives discussed above, the emphasis here is not primarily on mass balance, but rather on processes and interactions.

The hypolimnia and surface sediments of the large lakes of the world range from perennially aerobic systems like the subarctic and upper Laurentian Great Lakes to permanently anaerobic African Rift Lakes. Basins with seasonal hypoxia like Lakes Victoria, Albert, Edward, and Lake Erie bridge these conditions. This spectrum provides a unique opportunity to examine the reactions which control iron-phosphorus geochemistry and the geochemical buffering of the phosphorus system. Such controls are important in softwater lakes but have not been examined in alternate aquatic environments. The oxides of iron and manganese are active sorption sites. Redox-triggered solubility reactions like the aptly termed "ferrous wheel" and manganese refluxing at sediment-water interfaces are important to geochemical fluxes.

Stoichiometric Relationships

The stoichiometric ratios of biologically important elements in the seston may become a most powerful tool for comparing lake processes across gradients of time and space, and within and between ecosystems. The phytoplankton present integrated C:N:P:Si ratios that can be extremely diagnostic, but this tool has not been developed and exploited. Unlike in the oceans, where the mean Redfield ratio is often assumed valid, there is good reason to expect revealing differences when large lakes are compared. Investigations based on stoichiometries have several useful features and unique potentials, which include:

a) indicating relative loading rates of different nutrients
b) identifying potentially limiting resources for phytoplankton
c) identifying biological intervention into biogeochemical cycles
d) ease of sampling and sample storage
e) standardized analytical methods for C, N, P, and biogenic Si.

The approach also reduces the need to identify and count organisms, although one must not forget that the changing stoichiometries are reflecting a changing species composition of the biota. Aside from the loss of biological detail, there are other drawbacks as well, the chief one being contributions from detritus. The extent of this problem has not been investigated in a systematic fashion, but it is possible that it may be overcome by corrective measures. In spite of the present difficulties, the approach holds such promise for successful inquiry that it deserves serious research effort.

INSTITUTIONAL ARRANGEMENTS AND FACILITIES

Institutional structures that presently exist, like IJC, are not designed to cope with the management of large-scale scientific initiatives. A sustained program of research on great lakes must include structures which provide scientists with the necessary institutional framework to manage long-term monitoring, coordinate research activities, store and maintain databases, and secure funding.

Present and planned satellites are adequate for water bodies at the size scale of great lakes. A regional database for imagery is needed to provide scientists with the information. Surface reference data will be unavailable at times owing to weather and seasonal obstacles to navigation.

Although there are many small vessels on the Laurentian Great Lakes, only one is supported by UNOLS and access to stations is generally difficult in seas approaching 2 m, which are a common occurrence for more than one half of each year. Research vessel availabilities on land-locked great lakes are virtually non-existent.

Remote Monitoring Devices

Programmatic needs for measuring chemical fluxes and biogeochemical cycling require the development of remote monitoring devices for several physical and chemical parameters, chlorophyll, transmissivity or particle distribution, current speed, and current direction. Deployment of such instrument packages at reference sampling stations in large lakes will provide the required long-term and frequent data sets that will permit the assessment of mean fluxes and the time scales of variability in the data.

At present the U.S. EPA, state DNRs, and Canadian federal and provincial agencies maintain assorted monitoring programs on the Laurentian Great Lakes. These programs are concerned primarily with indices of water quality from the viewpoint of eutrophication control or public health. Sampling is neither sufficiently frequent nor strategically timed to produce the data needed for resolution of biogeochemical research issues. It is very likely, however, that the improved communication that would be fostered by new institutional arrangements could promote many economies of data acquisition and synthesis.

5. LAND-WATER INTERACTIONS AND PALEOECOLOGY

PROBLEM DEFINITION

Records of long-term temporal variability are necessary to assess both natural and man-caused changes in ecological systems, particularly with regard to climatic changes and associated biological responses. Current efforts to predict potential climatic responses to increasing levels of atmospheric CO_2 and CH_4, for example, require direct evidence of climatic trends and associated biospheric conditions during the Pleistocene and Holocene. The paleo-records provide baseline reference and permit projections based on analogy. In the cases of other man-caused perturbations, such as eutrophication or acid deposition, detailed time series are necessary to trace the severity of the effects and to identify responses to mitigation. Long-term records of species composition and metabolic processes such as primary and secondary production can provide perspectives on biological and evolutionary changes within ecosystems.

Large lakes integrate regional watershed and airshed conditions. They represent mesoscale systems that bridge local conditions with continental and global scales. Within the sediments of the world's large lakes are records of current and ancient environmental conditions. The information buried there has been virtually unmined. To interpret the multifaceted evidence preserved in the sediments requires detailed understanding of modern ecological and geochemical processes. In turn, information gained about historical changes in a lake and its watershed, or about regional climate, becomes a great aid in deciphering modern ecological conditions.

Watersheds interact with large lakes primarily via riverine inputs of dissolved and particulate matter. Nutrients, suspended clays, and dissolved or particulate organic substances are supplied to the lakes as functions of definable drainage basin characteristics. Although in large lakes the inputs are often small relative to the quantity of material stored in the lakes, the inputs can have profound biological consequences. This is particularly true of anthropogenic nutrient loads and toxic pollutants. Not just the magnitudes of inputs are important, but so is their timing. Fluvial inputs synchronized with vertical mixing or with reproductive phases of aquatic organisms can have widespread and amplified effects. Most watershed interactions are probably confined to coastal zones, but a variety of transport processes (Chapter 3) guarantee that the offshore regions are not thoroughly insulated.

RESEARCH GOALS

The principal goals of studying lake-watershed interactions fall into two categories. The first goal is to predict and model the hydrologic and material loadings to lakes from surrounding regions in order to complement biogeochemical investigations of the lakes. These efforts also permit judgments to be made about the likely effects of perturbations in the drainage basin with regard to water balance, nutrient loading, and trophic condition. The second goal is to assemble a modern calibration standard for reading the paleoecological record preserved in the lake sediments. The relationships between ambient conditions of productivity, terrestrial vegetation, species composition, and the fossil traces of these properties must be established with sufficient reliability to make the record intelligible.

EMERGING RESEARCH OPPORTUNITIES

The growing availability of detailed information about land use, vegetation cover, and topography derived from remote sensing provides a special incentive for studies of lake-watershed interactions. Changes within drainage basins owing to development, deforestation, or natural catastrophies can be quantified as to magnitude and areal extent. Large lakes provide the appropriate scales to integrate regional phenomena, and they match well the spatial resolving power of present remotely sensed data.

RECOMMENDED RESEARCH INITIATIVES

Long Cores from Ancient Lakes

Efforts to obtain and analyze long cores from ancient lakes like Baikal, Tanganyika, and Malawi are of highest priority. Ancient lakes offer an unparalleled potential for resolving millions of years of the earth's history year by year or decade by decade. Such detailed temporal resolution is not possible in the ocean because sedimentation rates are slower there, and because sediments are mixed too well by large marine invertebrates. The only other sites capable of yielding comparable resolution are polar ice fields, but the potential of the latter to yield biological data is minimal.

Detailed analyses of deep lake cores are appealing on both practical and theoretical grounds. Ecosystems are sensitive to rare catastrophic events which occur at frequencies that have never been assessed. Unearthing a spectra of variability that range from years to millions of years would have great theoretical value in ecology. The historical records in the sediments can reveal a background account of regional climate, hydrology, and resource supplies over evolutionary time scales. Many ancient lakes have high degrees of endemism, and considerable species radiation has occurred within single basins. Taxa with fossil records can be examined directly for evidence of speciation or stasis. These lakes offer a unique opportunity to test competing evolutionary theories of gradualism and punctuated equilibria under conditions where stratigraphy and temporal scales can be determined exactly. Furthermore, the long-term records of continental climate decipherable from lacustrine sediments invite key tests of models of paleo-climate derived from ocean sediments and global simulation models. The lakes are particularly valuable in these tests because they are in more intimate contact with terrestrial environments than are the oceans, and the effects of climatic changes on terrestrial systems are of primary interest to man. The paleo-climates of East Africa assume special interest because of the interlacustrine African origin of early man.

Integrated Watershed Studies

Large lakes and their watersheds constitute integrated biogeochemical systems. The influences of fluvial and atmospheric inputs on productivity and biomass should vary in a predictable manner with hydrologic residence times. For many large lakes such budgets are poorly known, but they must be constructed in order to calculate mass flux budgets. Among the Laurentian Great Lakes the water residence times are well known, and they vary by

one hundred fold from Lake Superior to Lake Erie. These lakes consequently provide an excellent system in which to examine effects of residence time. Further comparisons should be sought through a broader survey of large lakes that range from rapidly flushed mouth bay lakes in the Amazon to intermittently closed basins like Lakes Tanganyika and Malawi.

Inputs of water, nutrients, and suspended sediments establish horizontal and vertical gradients which are especially amenable to study in large lakes. Seasonal differences in inputs add a temporal component to the heterogeneity. The ecological and biogeochemical implications of the gradients are considerable because they are the "fronts" where lake-land interactions occur. Availability of nutrients and light, and thus patterns of primary productivity, may be affected by interactions among the solutes, particles, and physical mixing. Studies of these phenomena are thus tightly linked with initiatives proposed in Chapter 3 (Scale Dependent Processes and Influences) and in Chapter 4 (Chemical Fluxes and Biogeochemistry).

INSTITUTIONAL ARRANGEMENTS AND FACILITIES

Several recent innovations in oceanographic instrumentation and institutional arrangements must be adopted in order to initiate research on the paleoecology of large lakes.

In Situ Devices

Long-term moorings of modern sediment traps that permit measurements of episodic deposition and size distributions of the sedimenting particles are a high priority. Trap collections should be related to ongoing monitoring of particle dynamics in lakes. Remote robotic samplers capable of obtaining cores with the sediment water interface undisturbed are necessary to evaluate early diagenic processes.

Side-scan and multibeam sonar systems are needed to construct detailed maps of lake bottoms and to locate features like underwater vents, erosional channels, and other diagnostic topography. Effort should be expended to produce portable devices which can be deployed from vessels of opportunity on land-locked great lakes. Such a system, moreover, should be installed on a UNOLS vessel assigned to operations in the Laurentian Great Lakes. High resolution seismic profilers are needed to guide the site selection process for deep cores.

Deep Coring Technology

The technology for raising long cores from deep water is well developed in NSF's Deep Sea Drilling Project and in the commercial oil industry. The challenge is to transfer this technology to land-locked lakes in remote areas. Major concerns include protection against striking pressurized oil or gas deposits and the large overall cost of the effort. Coordinated, multi-institutional, international efforts that combine the expertise of both universities and industry are needed.

Remote Sensing Technology

Application of current and planned satellite-borne remote sensing technology permits the examination of large lakes and their watersheds as ecological units. The present obstacles to progress are the lagging development of geographic information retrieval systems and implementation of automated ground based data collection and distribution. The necessary support facilities will require long-term investments by funding agencies and an expanding user community of limnologists trained in the new techniques. Specific endeavors that require immediate, active support are the use of the ocean color imager (OCI) and the Earth Observing System (EOS) for limnological applications. For scientific purposes an important element of a space-based sensing system is data distribution. As sophisticated sensors transmit increasing amounts of data, their availability to limnologists will require improved institutional facilities and trained personnel.

6. FOOD WEBS, COMMUNITY STRUCTURE, AND TROPHIC RELATIONS

PROBLEM DEFINITION

Present understanding of aquatic ecosystems is based largely upon experience with small, geologically young lakes and large, ancient oceans. Limnological investigations often seek to explain how species interactions and environmental conditions influence community structure and ecosystem functioning. The goal remains elusive because rapid rates of seasonal change, interactions among pelagic, littoral, and benthic regions, and transient watershed influences confound the analyses. Restricted faunal representations of zooplankton and fish species in individual small lakes compared to the species suite present in an entire geographic region also make generalization among systems more tentative. Oceanic studies have emphasized other goals, owing to technological and institutional constraints. The financial and logistical expenses of ship time have dictated that oceanic studies be infrequent, "snapshot" surveys with long intervals between repeat visits. Research questions have thus focussed on processes such as the rate of primary production in the sea, the fate of the particulate matter produced, sedimentation rates, and resultant effects on the biogeochemical cycle of carbon. Studies at the population and community level in oceans have typically been restricted to descriptions of food web structure and attempts to explain biogeographical distributions. Questions about population dynamics and community interactions are frustrated by the low frequency of sampling, the heterogeneity of water masses, and the phyletically diverse, species-rich marine biota that are very patchy in both space and time.

Major advances in scientific knowledge often result when hypotheses evolved in one system are used to predict phenomena in other systems that differ significantly in scale or composition. Comparison studies among the great lakes of the world offer unique opportunities to improve our understanding of the structure and function of both freshwater and marine ecosystems. The lakes offer an unparalleled range of geological ages, from 7,000 to 60,000,000 years, and a diversity of such characteristics as depth, temperature, biotic diversity, trophic status, and chemical composition. The antiquity of some of the lakes is particularly important because the time scales are large enough for the systems to express the phenomenon of species evolution. Nonetheless, species richness remains generally low in these lakes compared to the oceans, and thus they present the best opportunities for forging a link between marine studies and population or community-based lake investigations.

Great lakes exhibit nearly the full range of physical phenomena present in the ocean, and the water masses can be sampled repeatedly. Their plankton and fish communities are more species rich than those of small lakes but they lack the daunting phyletic diversity of the oceans. The physiologies, life cycles, and autecologies of the species present are better known than those of marine systems. The fisheries of the Laurentian Great Lakes, at least, constitute well-defined systems with high enough levels of exploitation to study the influence of stock management practices

on commercial catches, to investigate multispecies interactions, and to evaluate trophodynamic models of potential yield.

The ancient, relict lakes, particularly Lakes Baikal, Tanganyika, Malawi and Victoria, show considerable evidence of species evolution. The cichlid fishes of the East African Rift lakes, for instance, arguably represent the most spectacular radiation of a vertebrate group on earth. Efforts to learn how particular taxa express such diversity may be rewarded with great knowledge about the process of biological speciation. Although these communities are unique world heritages, they are at risk and may be presently disappearing. The introduction of an exotic piscivore to Lake Victoria has reduced the numbers of many unique endemic species. From a scientific point of view, the case now provides a modern experiment in massive species extinctions.

RESEARCH GOALS

The ultimate goal of research on the large lakes of the world should be to develop a coherent, integrated, and predictive framework for community structure and function in relation to large scale features of the physical and biogeochemical environment. This goal is possible in great lakes and perhaps nowhere else, because the features don't exist in small lakes, and because repeat sampling of communities is difficult in the ocean. Immediate goals involve multidisciplinary efforts to decipher complex interactions. Much of the progress we seek can result only from close coordination of efforts among biologists, biogeochemists, and hydrodynamicists. Although each discipline can engage individually in fundamental and innovative inquiries, great lakes are far more conducive to true interdisciplinary research than either small lakes or oceans. This is because in these other systems one discipline often becomes the "handmaiden" of another, either because biological peculiarities are so important in small lakes, or because the physical regime so dominates oceanic phenomena.

Physical oceanographers have bridged the temporal gaps between cruises by deploying moored in situ sensors and by using synoptic satellite surveys. Biologists can adopt similar sampling strategies to address some aspects of community level questions in large lakes. The Laurentian Great Lakes are good systems in which to develop such new technology and to unify the foci of freshwater and marine studies.

EMERGING RESEARCH OPPORTUNITIES

An excellent opportunity to understand ecological processes in aquatic systems is the chance to view great lakes as comparative, natural "experiments." The comparisons can be among the different great lakes themselves, or across a gradient of basin scales from small lakes to largest oceans. Important links between biotic and abiotic phenomena may emerge by this approach. The areas most amenable to study range from processes operating at the base of food webs to those at the apex, and on time scales from generation times of single organisms to those of evolutionary change.

Most research opportunities are products of the spatial and temporal scales provided by great lakes, or by the correlated uniqueness of the fau-

nas of the lakes. Differences in the fundamental properties of food webs among great lakes provide testing grounds for hypotheses about the evolution of aquatic food web structure. Not only do the tests have fundamental scientific value, but they can help decipher interbasin variation in economically important features like fish yield and resilience to exotic invasions. Plankton communities of the lakes often differ little in species richness whereas dramatic differences exist in the radiation and endemism of nearshore and benthic communities. This makes it possible to study differential speciation and comparative food web complexity even in a single basin.

Food webs in ancient lakes may have higher energy transfer efficiencies than those in young lakes. Both Lake Tanganyika and the North Sea have much higher fish production per unit primary production than the Laurentian Great Lakes (Fee and Hecky, Appendix B1). This suggests that food webs may function differently after long periods of evolutionary accommodation. The generality of this finding needs to be tested, and thus endorses the general goals of biogeochemical studies (Chapter 4). Accurate productivity measurements for large lakes are needed, as are carbon turnover rates and mass balances for carbon and nutrients. The relative importance of resource limitation and of predatory exploitation in regulating community-level processes also require study because approaches based only on energy flow do not provide satisfactory representations of these communities. Energy flow between trophic levels is unidirectional, whereas bidirectional food web interactions influence the rate of flow and how the energy is packaged. Quantitative investigations of species interactions, and construction of biomass size spectra (Sprules, Appendix B5) can help identify if food webs differ among great lakes. Even the opportunistic use of heavy metal contaminants as tracers for trophic transfer efficiencies has value as an explorative tool. The general topics of investigation revolve around transfer efficiencies, food chain lengths, growth efficiencies, and predatory capture efficiencies.

Species richness of planktonic algae is similar in old and young lakes, but zooplankton communities of old lakes are simplified, and fish communities are much more diverse in ancient lakes. The patterns evoke questions about food webs and factors which influence evolution. They imply that the magnitudes of diversity are not dictated by the primary producers or the production base. The relative contribution of cladoceran and copepod species to freshwater communities appears to depend on lake size, with copepod dominance increasing in larger lakes. Experimental studies of the invasibility of these communities are feasible, and some large scale natural experiments are presently underway.

RECOMMENDED RESEARCH INITIATIVES

Nutrient Cycles

Studies of mass and material flux often treat the ecosystem as a compartment or box which contains the element of interest. This may be an appropriate first step in the construction of budgets for carbon, nitrogen, and other elements, but it is an approach which yields minimal information about ecosystem biology. Biogeochemical investigations provide necessary but insufficient information about the functioning of aquatic ecosystems.

Budgets can identify the magnitudes of particular fluxes, but not why they came to exhibit those particular values rather than others. This difficulty is especially true in the case of prolonged retention of nutrients within the mixed layer by recycling processes.

The relative contributions of metazoan versus microbial metabolism, as well as the types of organisms present, can influence recycling rates. Small, productive lakes tend to be dominated by cladocerans that produce uncompacted feces which remain in suspension and host microbial activity. Productive oceanic regions, in contrast, are dominated by copepods, euphausids, or other groups which produce fecal pellets with high sinking velocities. In lakes, copepods dominate in more oligotrophic habitats. The degree of nutrient recycling in the mixed layer as opposed to export of nutrients in particulate form through the pycnocline is probably controlled by the types and abundances of zooplankton and the thickness of the mixed layer. The Laurentian Great Lakes offer a chance to test this hypothesis because they present a gradient from copepod dominance in the upper lakes to cladoceran dominance in the lower lakes, and because population densities, mixed depths, and mean water column temperatures vary among basins and sub-basins.

Nutrient Limitation

The application of a mass-balance approach to phytoplankton nutrient demand:supply ratios has often led to the superficial generalization that lakes are "phosphorus limited" while oceans are "nitrogen limited." Whether this is true, or why it should be true, is not presently known, and there is yet no body of theory that satisfactorily unifies freshwater and marine observations across a broad range of physical, chemical, and biological circumstances. A coherent theory of nutrient limitation would benefit enormously from an integrative approach to both marine and freshwater systems. Comparative studies using comparable techniques are needed to evaluate the universality or uniqueness of resource limitation in aquatic ecosystems.

The concept of nutrient limitation and the methodologies employed should be thoroughly re-examined. It may now be appropriate to supplant the single limiting nutrient paradigm using techniques with greater precision than bulk bioassays. Present understanding does not permit an unambiguous prediction of the status of nutrient limitation in lakes or oceans. Because the degree of coupling between offshore regions and terrestrial or littoral processes is a decreasing function of lake size, regenerated nutrients must be more important in large lakes. One line of reasoning holds that great lakes should tend toward limitation by N because it is less rapidly regenerated than P. Offshore phytoplankton might thus display less variability because resource supply rates are dominated by regenerative processes. Nearshore zones might more closely resemble smaller lakes in their resource limitation characteristics. These predictions, that offshore waters of great lakes and the oceans should tend toward nitrogen limitation, contrast with other lines of reasoning, and with direct observation.

Lake ecosystems can import carbon and nitrogen from the atmosphere when demands exceed supplies, and this ecosystem phenomenon leads to the

evolution of phosphorus limitation in lakes. A natural question is whether this also happens in the oceans. It may be that only perturbed coastal ocean regions are nitrogen limited and that the open ocean is co-limited by both phosphorus and nitrogen. Alternately, if the oceans are genuinely nitrogen limited then what are the processes that have prevented nitrogen fixation on a scale sufficient to correct the shortage? Two hypotheses relevant to this fundamental issue can be tested best in great lakes.

The first hypothesis is that low organic carbon levels in oligotrophic ocean waters preclude the formation of anaerobic microzones necessary for nitrogen fixation. This could be tested by measuring fixation rates in a lake with a low N:P ratio and low organic carbon, such as Lake Tanganyika. The second hypothesis is that high turbulence levels in large water bodies preclude the colonial and clumping geometry essential for microzone formation. This hypothesis could be evaluated in western Lake Erie during periods of low N:P ratio and high wind.

Finally, the single limiting nutrient concept may be too simplistic. Variance around the well-known relationship between spring phosphorus and mean summer chlorophyll can be reduced by consideration of the N:P ratio (Smith, Appendix B3) and it is likely that other essential nutrients such as silicon (for diatoms) influence production as well. Great lakes present a gradient of N:P:Si stoichiometries that should facilitate studies of nutrient limitation by offering natural experiments in nutrient loading rates, and thereby they offer a fine laboratory in which to advance understanding of the underlying mechanisms.

Community Structure

Aquatic ecologists presently debate the relative importance of predation processes versus resource supplies in determining community structure. They ask how species specific reproduction and death rates combine to produce observed community structure, and to what degree steady state models can predict community structure in variable environments. Great lakes probably offer the only good places to address these fundamental questions because they encompass hydrologic flushing rates from two years to centuries and consequently a gradient in degree of approach to steady state. Within each lake a further gradient in approach to steady state exists as one compares dynamics of nearshore to offshore regions. Resource competition theory should prove most effective in predicting community structure in the lakes with the longest turnover times and in the offshore regimes of each lake. Great lakes thus constitute excellent working systems in which to forge better links between theoretical ecology and empirical observation.

Large lakes in temperate regions possess a unique physical phenomenon during the spring warming period which provides a tool for studying the influence of physical factors on community structure. Continued mixing in the cold central portion of the deeper lakes delays stratification a month or more relative to shallower, inshore regions, and a convective regime called the "thermal bar" consequently develops. This condition subjects an initially homogeneous plankton community to quite different combinations of light, temperature, nutrient supply, turbulence, and grazing pressure in

different regions of the lake. This novel characteristic of large lakes makes them particularly useful for investigating how these environmental factors contribute to the development of biological communities.

Another contentious subject is how community structure is measured. Aquatic communities have been characterized in ways ranging from species identification and enumeration, through characterization by broad taxonomic or functional categories, to determination of particle size spectra. No one method is "best"; the optimal method of study depends upon the nature of the question being asked. Some interactions between organisms are influenced primarily by size relationships, some by physiological or physical characteristics that can be best summarized by taxonomic or functional categorization, some by species-specific cues, and still others by behavioral patterns or habitat preferences that are not adequately incorporated into current models and conceptual constructs. This latter shortcoming is highlighted by a reciprocal transplant experiment involving planktivorus minnows and piscivorous bass (Carpenter and Kitchell, Appendix B4). The expected increase in planktivory in the lake receiving the minnows was not observed because, unexpectedly, the minnows abandoned the pelagic region in order to avoid the few remaining piscivores. Small scale experiments are useful in demonstrating how mechanisms operate but only large scale experiments demonstrate which mechanisms are important. Studies of the great lakes should prove invaluable in evaluating the burgeoning corpus of ecologic theory that has grown from observations in small lakes and from short-term manipulation studies.

The Laurentian Great Lakes constitute very large scale, long-term manipulation "experiments" that are already underway. Unfortunately, the present level of monitoring and research activity is inadequate for science to extract full benefit from the opportunities at hand. The introduction of salmonids into Lake Michigan, for example, is a massive manipulation of community control forces, the effects of which are currently affecting the food chain. The resultant decline in alewife populations and consequent reduction in planktivory has led to a resurgence of large daphnids and presumably a shift in the magnitude and nature of grazing pressure on the phytoplankton. This is merely the latest in a multitude of introductions, extinctions, and environmental manipulations that the lower great lakes, in particular, have experienced. The buffering effect of large size makes these lakes especially amenable to study because the rate of change should be slower and the duration protracted. The responses of the diverse biota in these lakes should permit better understanding of such ecological phenomena as species substitution, community resilience, stability, and persistence.

<u>Physical-Biological Interactions</u>

The physical dynamics of large lakes differ fundamentally from those of small basins, for reasons explained in Chapter 3 (Scale Dependent Processes and Influences). If physical forces intervene significantly into biological realms, the structure and function of communities in large lakes should differ from those in small ones. Greater depths of mixed layers in great lakes may influence the efficiencies of nutrient cycling and microbial activities, and they may lead to light limitation more readily than in

small lakes (Fee and Hecky, Appendix B1). Both surface irradiance and vertical spectral distributions must be measured for great lakes. Suitable instruments are available, but they have seen little use. The information is vital for remote sensing applications. The diversity of subbasins, river plumes, and scales of patchiness in large lakes moreover provides a set of adjoining, heterogeneous growth environments for organisms with differing environmental requirements. The subsystems undoubtedly provide multiple sources of innoculae to the pelagic community, where the innoculae may or may not sustain viable populations.

Among the fish, especially, biological processes in large basins are different from those in small systems. The ability of predators to control prey populations and the abilities and strategies of prey to avoid predators depend on lake size. In large lakes, predators often restrict their search patterns to particular habitats. Prey may change from seeking specific structural refugia to behavioral techniques like schooling. Differentiation of thermal habitat niches is more likely in great lakes because of the expanded scale of the habitats. In small lakes, individual thermal regions within the metalimnion, for example, may be too small to support a specialized population. Another feature of large lakes is the emergence of genetically identifiable fish stocks. Such independent stocks do not arise in small lakes. In the ocean the contribution of individual stocks to the whole population is difficult to assess. But in great lakes it is possible to examine the rise, dynamics, and interactions of stocks and to relate the findings to evolution and speciation.

The importance of physical forces on the biological communities in large lakes must be assessed at several scales of space and time. Appropriate scales and phenomena have been identified in Chapter 3.

Investigations of the African Rift Great Lakes

Perturbations of the ancient great lakes of the African Rift offer very special, fleeting opportunities to document the effects of exotic introductions into highly diverse communities. These lakes are characterized by extreme levels of endemism owing to antiquity and millenia of isolation. Extinctions of hundreds of cichlid species may be underway following the introduction of Nile Perch (*Lates niloticus*) to Lake Victoria. Thoughtful documentation of these changes, and those associated with future inevitable introductions, should be of more than academic interest to a society that is struggling with the issues of massive watercourse diversions and creation of new types of organisms through genetic engineering. Both situations produce circumstances where species and communities are confronted with competitors and predators that are outside the range of their evolutionary experience.

INSTITUTIONAL ARRANGEMENTS AND FACILITIES

Present ability to assess and interpret changes in community structure in the Laurentian Great Lakes and in East Africa is handicapped by two limitations. First, historical data are piecemeal, scattered, and often inconsistent. Few long-term data exist, and too little has been done to promote their importance. Second, the tools for assessing population abundances of fish, in particular, are not widely available on great lakes,

although adequate technology does exist. The second limitation is the easiest to remedy.

Deployable Measurement Systems

A fleet of moored instrument cluster systems should be developed for project-specific deployment on a shared basis among investigators. Automated and standardized data collections for reference properties such as light, fluorescence, and particle density will encourage comparative investigations and strengthen their findings. Particular attention should be paid to the development of devices for automated sampling and preservation of biota so that offshore biological research programs need no longer be limited by the infrequency of ship-sampling. For example, inexpensive syringe samplers designed for marine water chemistry could easily be adapted for phytoplankton and bacterial sampling while pump systems currently utilized for bioluminescence studies in the ocean might be adapted for automatic zooplankton sampling. Ongoing refinement of acoustic technology offers the prospect of automated and horizontal profiling of zooplankton-size particles. Advances in microcomputerization and telemetry networking should enable instrument cluster interrogation by shore stations or satellite which would, in turn, permit real-time data analysis. The instrument clusters should require only infrequent vessel servicing for retrieval of preserved specimens and power pack replacement.

Significant improvements in fish sampling techniques are now technologically feasible. The most pressing needs are for abilities to measure true fish abundances, size structure of the fish communities, and scales of patchiness. New underwater acoustic techniques can satisfy these needs but they have not been widely used in lakes. An automated system for deployment aboard a UNOLS vessel is certainly justifiable for the Laurentian Great Lakes. In addition, a portable system must be developed which can be deployed reliably from diverse vessels on land-locked great lakes of the world.

Long-term Data Collection

Reference sampling stations and reference measurements should be established for the Laurentian Great Lakes and for other great lakes where access is technically feasible. Efforts to implement Long-Term Ecological Research Programs should be coupled with a data managing and data archiving structure maintained for scientific use, much like a professional library or well-curated research museum.

A1. PLANKTON ECOLOGY

IMPORTANCE AND ROLES OF PLANKTON

Planktonic organisms are responsible for the primary production in pelagic environments, as well as the dominant primary consumption of this production. They constitute the base of food webs, and they regulate the mass flux of carbon, nutrients, and trace substances between dissolved and particulate phases in the water column.

Great lakes possess relatively isolated planktonic communities which occur during stratified seasons in temperate habitats and perennially in offshore regions of meromictic great lakes. They are amenable to frequent sampling in a cost-efficient manner. Plankton communities of large lakes are not, however, isolated from coastal and littoral regions for long periods relative to evolutionary processes, which may explain the floristic and faunistic similarities of phytoplankton and zooplankton from large and small lakes. The fact that Great Lakes plankton experience stochastic upwelling and littoral incursions provides natural experiments of community perturbations and resilience.

Freshwater plankton have reduced species richness compared to oceanic plankton, which simplifies studies of food webs and interactions among species.

Great lakes world-wide, and the Laurentian Great Lakes in particular, are experiencing perturbations through nutrient and contaminant influxes as well as introductions of fish and zooplankton that permit large-scale tests of current theories about community construction.

Great lakes differ with regard to nutrient loading, basin morphometry, age, and latitude and so offer the chance to compare communities and test hypotheses about community-level processes. There is also at least some potential for replicability among great lakes for these characteristics individually.

DOMINANT RESEARCH CHALLENGES

Food Web Comparisons Among Great Lakes and Other Aquatic Systems

Alternative food webs can affect interbasin variations in fish yield as well as system resistance to exotic invaders. Although there is much species overlap between small and great temperate lakes, there is a shift in dominance among zooplankton from cladocera to copepods with increasing lake size and oligotrophy, and there is also a significant increase in species richness.

Food webs in older aquatic ecosystems may have higher energy transfer efficiencies than young ones. The phenomenon may arise either because food chains are shorter, growth efficiencies are higher, capture efficiencies are higher, or because the communities are more co-evolved. The alternatives should be investigated by

a) measuring primary and secondary productivity
b) collecting detailed feeding ecology data
c) evaluating biomass size spectra and trophic energy relationships.

Species richness of planktonic algae is about the same in old versus young lakes, while zooplankton of old lakes are less diversified, and fish exhibit much greater diversification than in young great lakes. Ancient lakes may have fewer pelagic zooplankton species because the assemblages are resistant to invasion.

One test would be to determine whether exotic algae or zooplankton species can invade these assemblages in micro- or mesocosm enclosures. Successful invasions would suggest that low colonization rates maintain low species diversity. Unsuccessful invasions would imply that highly co-evolved species constitute a community resistant to invasion. Alternatively, food web models constructed from feeding data may predict that the systems are resistant to invasion.

Large, oligotrophic lakes may favor copepods because they survive better at lower food concentrations. Their long generation times may make copepods ineffective at exploiting variable food resources and put them at a disadvantage in small lakes with high temporal variability in food levels. Large lakes may discourage species like cladocerans that commonly produce resting stages. Variance spectra for food supply should be assembled for lakes of different size and trophy. The relative strengths of correlation between mean food concentrations, their variances, and the copepod/cladoceran ratio may point the way to definitive experiments. The proportion of reproductive effort committed to resting stages as a function of lake size or productivity may help interrogate the third possibility.

Material Fluxes Among Trophic Levels

Accurate productivity measurements from large lakes are needed to establish both carbon turnover ratios and mass balances for carbon and nutrients. Variabilities in the relationship of photosynthesis rates to irradiance must be determined as prerequisite to eventual satellite-derived productivity estimation.

One theoretical means of maintaining structure in phytoplankton communities is through resource competition along ratio gradients. If this mechanism is prevalent in nature, different phytoplankton communities should have different stoichiometries for nutrient elements. When nutrient limitation controls the growth and turnover rates of populations, stoichiometric characteristics can change with growth rates even if the nutrients are supplied in constant proportions. In light limited populations, however, the stoichiometric composition of the plankton should directly reflect the net supply rates of nutrient elements to the mixed layer. Great lakes are more likely to exhibit light limitation of phytoplankton than are small lakes because mixing layer depth increases with lake size and fetch. The degree of light limitation in different great lakes needs study not only to interpret community construction rules, but also because it has applications in remote sensing. Productivity per unit chlorophyll should be higher in light-limited populations than in nutrient limited ones.

Coupling and Exchange Between Pelagic, Littoral, and Benthic Regions

Because of deep mixing and light limitation, primary production in great lakes may be closely coupled to meteorological conditions. The degree of coupling between the offshore mixed layer and terrestrial or littoral inputs should be reduced in these large lakes. The systems nonetheless exhibit a wide variety of physical structures and processes that couple the different, identifiable regions of the lakes. Particulate organic carbon, nutrients, and phytoplankton can enter the pelagic zone from nearshore sources. Weather conditions in winter or spring can alter loadings and transport between littoral or benthic regions and the pelagic sufficiently to influence patterns of succession and community development.

Plankton dynamics at thermal bars are particularly interesting. Thermal bars may be boundary regions where significant fractions of total annual productivity occur. They offer predictable study sites for investigating interactions between turbulence and phytoplankton morphological diversity or between vertical nutrient advection and primary productivity.

Subbasins and plumes in great lakes often have distinctive resource supplies and develop distinctive plankton assemblages. These may constitute useful subsystems to study population dynamics and resource-based community models. Such subsystems can provide innoculae for the pelagic community. Efforts are needed to determine if specific seasonal time windows, and directions of significant storm events, influence subsequent summer plankton assemblages.

Higher trophic levels in great lakes may be relatively insulated from the effects of perturbations to primary productivity. Short-term variability among the phytoplankton can be averaged out by the long development times of calanoid copepods and the size and strong mixing of the epilimnia. The stability of great lakes plankton communities needs careful attention to see if community properties evolve or emerge with basin scale. Such features may explain the persistence of high fish species richness in tropical lakes and the presence of glacio-marine relicts like *Mysis*, *Limnocalanus*, and *Senecella* in the Laurentian Great Lakes.

EMERGING TOOLS, TECHNIQUES, AND FACILITIES APPLICABLE TO GREAT LAKES RESEARCH

Monitoring Devices

Measurement systems which emphasize remote and automated techniques must be developed for great lakes applications. The systems should measure physical and chemical parameters as well as a set of gross biological properties of common interest to plankton ecologists. These include chlorophyll, total particle density, and particle size distributions measured often enough to discern diel patterns. Two design options are possible. Fixed stations could be established, in which case an institutional arrangement is necessary to gather, process, and disseminate the data. Alternatively, sets of deployable cluster systems could be held in a common pool and scheduled for use in response to specific experimental projects. The pool must necessarily be different from marine applications because of differences in buoyancy and depth calibration requirements. We favor the

second option because deployments in Africa, South America, and Asia would best be served by the great flexibility. Data should be transmitted via satellite in some systems and stored in place in others.

Remote Sensing

Satellite technology must be exploited to measure primary productivity of great lakes world-wide. The main obstacles at present are the long delays in obtaining imagery and the lack of calibrations between rates of photosynthesis and irradiance.

Tracer Technology

New applications of tracers, including isotopes, metals, and organic contaminants, are needed to measure trophic transfer rates and efficiencies.

A2. FISH ECOLOGY

IMPORTANCE AND ROLES OF FISH

Fish communities constitute the apex of food webs in great lakes, and usually consist of planktivorous, piscivorous, and benthic-feeding species. They include components of high commercial value, and in some regions they supply valuable protein to the indigenous human populations.

The world's great lakes possess characteristics uniquely suited to address basic issues about fish ecology and the processes affecting fish community structure and function. Great lakes differ from smaller lakes in four significant ways:

a) Great lakes have truly pelagic systems with reduced nearshore and nearbottom "edge effects."
b) Great lakes systems are subject to large-scale physical and biological processes.
c) Great lakes present large gradients in age and latitude, hence large differences in seasonal temperature and light regimes.
d) Great lakes have deep benthic communities.

Oceanic systems share these properties but great lakes have well-defined boundaries with measurable inputs and outputs. Because of the boundedness of the world's great lakes, questions can be addressed at the population, community, and ecosystem levels. Comparisons of benthic and pelagic processes can be made within and among great lakes. For example, it may be possible to assess the impact of small-scale events (e.g., fronts) or short-term episodic events (e.g., upwelling) on whole, definable biological systems. Additionally, the great lakes have unique properties of spatial scale, temporal variability, and minimum stability that impose special constraints on the fish communities.

DOMINANT RESEARCH CHALLENGES

Pelagic Processes

The relative influence of predation and resource limitation on the structure of aquatic communities is a topic of great current interest. Great lakes exhibit space and time scales that make these issues testable in pelagic environments, where spatial scale is a property of interest. For example, large lakes may have large scale refugia which would make it difficult for a predator to control its prey populations, or at least would require a different level of predator capture efficiency than would suffice in small lakes. Large scale mixing may also influence competitive interactions and the relative strengths of nutrient limitation and predation. Primary production and trophic energy transfer efficiency are probably affected by predation and, in turn, the effects of predation are constrained by primary production and transfer efficiencies. The questions of great immediate interest are the following:

a) Are pelagic systems and benthic systems differentially susceptible to predator control, and are they inherently different in trophic transfer efficiencies?
b) How do trophic interactions mediate the vertical fluxes of carbon and other elements in the pelagic zone?

c) How much are inshore/offshore and pelagic/benthic processes coupled?
d) What controls recruitment in pelagic fish species? How do different sources of mortality, from competition, predation, and starvation, affect recruitment of larval fishes?
e) What determines the time and space scales of biological patchiness among fish and plankton?

Large-Scale Physical Processes

The scale of great lakes creates differences in habitat heterogeneity and in the ratio of littoral to limnetic habitat that are unique to the large basins. Some addressable questions include:

a) How do large-scale physical dynamics affect biological processes at population, community, and system levels?
b) Are fine-scale (e.g., frontal) effects reflected at the systemwide level?
c) Are there more thermal niches for fish in the extended spatial coverage of thermal habitats in temperate great lakes?
d) What is the role of episodic events (e.g., upwelling) on biological populations or system level productivity at the higher trophic levels?

Large-Scale Biological Processes

Biological processes in large systems may be strongly influenced by factors of scale. In small lakes, for instance, a single predator may be able to roam an entire lake in search of prey. In large lakes, predators begin to restrict search patterns to particular types of habitat. In great lakes, the ability of a population of predators to control prey populations may require increased efficiency on the part of the predator. Likewise, prey strategies to avoid predation may change from use of specific structural refugia to behavioral techniques such as schooling.

Other examples concern the relative importance of competition and ontogenetic shifts in habitat by fishes. To date, most work on competition in fishes has been done on scales of 1 m to 10 km. In small lakes, competition for food might be important because fishes may use the entire system. In large lakes, there is enough space that species or different life stages of a species can truly segregate. For example, differentiation of thermal habitat niche is much expanded in the great lakes, and fish often select habitats based on temperature.

A similar type of scale effect concerns the integrity and independence of genetically identifiable stocks. Stocks do not develop in small lakes and the interdependency of stocks with respect to the whole population cannot be assessed in the open ocean. In the great lakes, it is possible to examine how changes in one stock affect other stocks and the population as a whole. These questions can be formulated as:

a) How does the increased spatial scale of great lakes affect predator-prey interactions at the behavioral and population levels?
b) How does the increased habitat heterogeneity in great lakes affect predator-prey and competitive interactions?
c) What is the integrity and independence of genetically identifiable fish stocks?

Evolutionary Processes

The extensive gradient in the age of great lakes invites studies of the evolution of fish communities. For example, if we compare the fish community of Lake Tanganyika to younger lakes such as the Laurentian Great Lakes, we note a much higher fish diversity, more pelagic predators and perhaps a higher transfer efficiency in the food web. Do these differences develop through evolutionary time or are other factors such as the biological isolation, tropical habitat, and level of environmental stability important? The world's great lakes vary not only in age, but they occur at all latitudes. The annual light regimes and lake water temperatures vary significantly at different latitudes. These differences present alternative hypotheses to explain some of the differences in fish community structure noted above.

a) How does species diversity, production, and trophic efficiency affect community stability and resiliency to stress including species invasions?
b) Why are pelagic fish communities in large lakes so low in diversity compared with marine ecosystems?
c) Have older systems developed higher efficiency in trophic transfer rates relative to primary production, and are systems with numerous trophic links inherently more (or less) efficient at energy transfer?

Deep Benthic Processes

In many of the world's great lakes the deep benthic fish communities live in a perpetually low-light and usually low temperature environment. The physiological adaptations to this habitat in terms of foraging strategies and bioenergetics are not known. The implications to rates occurring at population or community levels are also not known. Population processes and benthic-pelagic coupling can be addressed very effectively in bounded great lakes systems.

EMERGING TOOLS, TECHNIQUES, AND FACILITIES APPLICABLE TO GREAT LAKES RESEARCH

1. Significant improvements in fish sampling techniques are needed. State-of-the-art underwater acoustic technology is satisfactory, but has only recently been used in great lakes. Further technical developments are warranted.

2. Innovative measures or indicators of system level changes are needed. Promising approaches include paleolimnological characters, size structure of plankton and fish communities, hybridization levels in fish communities, and growth rates of long-lived fishes. Theoretical developments of trophic interactions and their effects on species richness are needed, particularly for tropical systems.

3. Good long-term data are so important that a Long-Term Ecological Research Program is needed in the great lakes.

4. Multidisciplinary collaboration is essential, particularly in the area of physical-biological coupling.

A3. MICROBES AND MICROHETEROTROPHS

IMPORTANCE AND ROLES OF MICROORGANISMS

Major Nutrient Cycling

Microbes cycle primary nutrients and control redox conditions in pelagic and benthic zones of lakes. The role of osmotrophic heterotrophs relative to phagotrophs in nutrient mineralization is not yet known. Bacteria use dissolved organic substrates as carbon sources, but interactions between dissolved organic materials and bacterial growth are difficult to quantify because ambient dissolved organics require sophisticated analytical detection and supply rates are often unknown. The relative importance of substrate limitation vs. grazer control has not been resolved for great lakes and measurements of bacterial production in the lakes are few. Little is known about factors that control bacterial growth rates and population sizes in aquatic systems.

The role of bacteria in pelagic nutrient recycling is probably determined by the organic substrates available. If the labile organic material is particulate, its ingestion and subsequent nutrient excretion by animals is likely to be a major mode of mineralization. On the other hand, if the labile material is dissolved, bacteria should be the major mineralizers. To determine the relative importance of different types of organisms to the recycling of photosynthesized material, better understanding of the forms, amounts, and fluxes of labile materials is required.

Interactions between autotrophic organisms and bacteria arise because autotrophs fix carbon that is subsequently used by heterotrophs, and they use nutrients remineralized by heterotrophs. Interactions between bacteria and larger heterotrophs arise because bacteria serve as a food source for some invertebrates. Bacteria accumulate dissolved organic matter in a form that can be ingested by protozoans and other phagotrophs.

Microbes influence nutrient dynamics in sediments, but the processes have not been well quantified in any great lake. Although ammonium tends to be the end product of organic nitrogen mineralization in anaerobic sediments, in the upper Laurentian Great Lakes, surface sediments are often oxic, and mineralized nitrogen is microbially oxidized to nitrate. Nitrate can be denitrified microbially or assimilated by phytoplankton. Quantification of these nutrient conversions in different great lakes, with varying degrees of nutrient enrichment and different morphological, thermal, and hydrodynamic characteristics, would elucidate the processes.

Transformations of different nutrients in great lakes reveal biological-chemical interactions. For example, the dissolution of silica fixed by diatoms is a chemical process not directly mediated by bacteria. Nitrogen mineralization to ammonium is mediated by both bacteria and animals, but subsequent conversions of mineralized nitrogen are strictly microbial processes. The mechanisms of interactions between phosphorus and microbes are still incompletely understood; the forms of phosphorus used by bacteria and phytoplankton and the potential competition between heterotrophs and autotrophs for organic and inorganic forms of P have not been

clarified. The relative importance of autolysis vs. bacterial breakdown of organic P compounds is not known for different lake environments. The study of phosphorus cycling mechanisms in the water and especially in the sediments is complicated by the strong tendency of phosphorus to adsorb chemically to particles.

Biogeochemistry of Great Lakes

In addition to cycling major nutrients and energy, bacteria influence biogeochemical cycles of other elements. Many highly specialized biochemical abilities are restricted to prokaryotes. Methane is an example of a compound whose formation and consumption is mediated by bacteria. After carbon is buried by sedimentation, biogeochemical cycling of carbon often includes methane as a major component. An important greenhouse gas in the global atmosphere, methane is the major vehicle for escape of buried carbon from freshwater sediments. It may accumulate in sediments and the water column or escape to the atmosphere. Methane is oxidized by aerobic methylotrophic bacteria in a chemosynthetic process, whereby some of the CH_4 carbon is refixed into biomass. The great lakes, including the highly productive African Rift lakes, are excellent comparative systems with a variety of different methane environments for study of such fundamental issues as:

a) What are the magnitudes of source and sink terms for methane?
b) How does CH_4 production affect carbon burial?
c) What amount of buried C is recycled to the biota via methanogenesis and methane oxidation?

Because of the global dearth of sulfur in great lakes systems relative to the oceans, comparisons between S cycling and carbon cycling in marine and freshwater sediments may be especially instructive. Sulfate reduction is often closely associated with methanogenesis, so differences between systems may help explain how tight the coupling really is. The nitrogen cycle includes other examples of uniquely microbial processes. Dissimilating NO_3 reduction removes NO_3 from the ecosystem in gaseous form (NO, N_2O, N_2); nitrification converts NH_3 to NO_3, and nitrogen fixation results in conversion of N_2 to organic nitrogen. The distributions and activities of organisms responsible for these reactions are not yet understood, but the dynamics of these groups probably influence nutrient limitation within and between lakes.

Microbes are also critical to the biogeochemistry of metals. Microbial plankton and bacteria are well known oxidizers of Fe and Mn, and are thought to have major effects on metal distribution and chemistry in aquatic environments. Many other microbes are capable of Fe and Mn reduction. These anaerobic bacterial processes result in the release of metals from sediments into the water column. The processes are linked to the establishment of anaerobic conditions, and thus to carbon sediment deposition and whole lakes carbon cycles. The Laurentian Great Lakes, with their metal-rich sediments and yearly mixing cycles, offer unique opportunities to study metal partitioning into major groups of the biota, and the effect of the biota on both the chemistry and distribution of the metals. Since the lakes are bounded systems, and most metals cannot be removed as volatile compounds, budgets for these elements can be obtained.

The biomass of biogeochemically-important bacteria is often small, and their growth rates are often slow, but the impact of the organisms in the chemical environment can be immense. Understanding the biogeochemical cycles that dominate each of the Great Lakes and predicting lake dynamics depends on understanding the microbial contributions and controls of the biogeochemical cycles.

Trophic Relations

A new paradigm of the ocean's food web has emerged in recent years, which may have parallels in great lakes food webs. Heterotrophic bacteria use 30 to 50% of primary production, via dissolved organic matter (DOM). Bacterial secondary production is consumed by a variety of protozoa, which in turn may be eaten by metazoans. This "microbial loop" constitutes a major pathway of material and energy flux in pelagic marine ecosystems. Views of the structure and function of marine food webs have been revised to incorporate these microbial processing steps.

Phototrophic picoplankton (cell size <2 μm) are significant in the annual carbon budget of both marine and freshwater ecosystems. It is likely, for instance, that as much as 60% of the primary production in great lakes owes to picoplankton, whereas most biomass determinations of great lakes phytoplankton have historically been based on larger green, bluegreen, and diatom cells. Large lake pelagic ecosystems are structurally identical to marine systems but they differ in functional relationships, like P vs. N limitation. These similarities and differences provide an unprecedented opportunity for collaborative and complementary work between limnologists and oceanographers.

As phototrophic picoplankton are grazed, they become either a source of regenerated nutrient or a source of organic C to the other consumers. The number and speed of multiple trophic transfers govern the efficiency of C transfer, and ultimately the efficiency of fish production. Long food chains or protracted residence times in individual components dissipate biomass as CO_2 and regenerated nutrients. The number of trophic links and their rates are unknown in all great lakes, profoundly limiting abilities to forecast fish yields from primary productivity.

Other members in this "microbial loop" include bacteria as well as colorless and photosynthetic eucaryotes that phagocytize cells ranging in size from minibacteria, 0.2 μm, to diatoms, 40 μm. Trophic-level concepts based solely on particle size are inapplicable in this system. It is critical to understand thoroughly the environmental forcing functions and biological factors controlling this newly-discovered carbon-nutrient pathway. At present, growth rates and selective grazing by protozoa, and relative competitive dominance among bacteria, cyanobacteria, and eucaryote phototrophs are very poorly documented. Therefore, links between the "microbial loop" and the "classical" grazing chain can only be surmised.

Thorough investigation of the microbial loop, in the context of the pelagic ecosystem as a whole, may result in a new paradigm of ecosystem structure and function incorporating not only carbon-energy flux but nutrient turnover as well. Research in great lakes on the importance of the microbial loop has just begun. However, it is already clear that there are striking similarities between the oceans and great lakes. The issues

raised in the marine work can complement the research in great lakes and also the great lakes may provide a better system for answering some questions relevant to both environments.

Autochthonous organic matter originates from phytoplankton and higher aquatic plants as exudates and products of autolysis, "sloppy feeding" by zooplankton, zooplankton feces, and pico-detritus, including colloids and polymers. Much of the autochthonous organic matter is produced through and mediated by inorganic nutrient enrichment of primary production processes. Allochthonous organic matter includes runoff from rivers and originates from agriculture sources as well as from terrestrial plants. Comparatively little is known about the pathways and influences of these different organic materials. Inquiries about organic matter cycling are relevant to management issues and eutrophication studies.

DOMINANT RESEARCH CHALLENGES

Organic Matter Cycling

The relative importance of autochthonous and allochthonous organic matter for bacterial production and nutrient cycling must be investigated in both nearshore and pelagic regions of great lakes. The sources of DOC that are supporting heterotrophy must be identified, and the time scales for degradation of both refractile and labile organic matter must be measured.

Biogeochemistry

The quantitative role of bacteria in nutrient cycling must be investigated over the spectrum of trophic states existing in great lakes. Because of the multi-trophic nature of organic flux via the microbial loop, it tends to be a predominant pathway of mineralization.

The roles of bacteria and protozoa in the decomposition of organic particles, and thence in the vertical flux of organic matter, can be elucidated especially well. Great lakes have the advantage of being bounded hydrodynamic systems, thus elemental budgets are more tractable than in the oceans.

Efforts are needed to quantify the relative importance of microbes vs. benthic animals in the mineralization and subsequent transformations of organic materials in the sediments, in basins of differing trophic state.

The N cycle, particularly denitrification, nitrification, and N_2 fixation, can be examined in great lakes in a fashion analogous to marine environments. Comparative data are virtually absent at present possibly because of the traditionally strong attention given to P limitation.

Microbial Trophic Relations

Comparison studies should probe the importance of the microbial loop to pathways of energy flow in pelagic regions of oligotrophic and eutrophic lakes. Great lakes provide a broad range of trophic conditions which should assist the comprehensive examination of this issue.

Too little is known about picoplankton production and utilization in great lakes vs. other larger lakes and marine environments.

Systematic variations in picoplankton processes may exist among systems. Unknown proportions of picoplankton production go into economically significant food chains. The biomass, metabolism, and ecological relations of these small photoautotrophs should be studied in detail.

The pathways of C, N, and P through microbial food webs may be different under P-limitation compared with N-limitation. The environmental factors that affect matter and energy flow, and which regulate bacterial growth rates, are potentially different in each case. The structure and function of food webs as energy links or sinks require serious attention.

EMERGING TOOLS, TECHNIQUES, AND FACILITIES FOR MICROBIAL STUDIES APPLICABLE TO GREAT LAKES RESEARCH

	Tool	Purpose
a)	^{3}H thymidine incorporation	Bacterial secondary production
b)	Fluorescent Acridine Orange Direct Counting	Enumeration
c)	Fluorescent beads and bacteria	Predation rates on bacteria
d)	Radiolabelling techniques	Nutrient uptake, assimilation, and transfer of bacterial matter up food chains
e)	Autoradiography	Identification of metabolic types of bacteria and picoplankton; determination of relative rates of nutrient processing and transfers in microbial communities
f)	Image analysis	Size distributions
g)	Video analyses	Documentation
h)	Flow cytometry	Enumeration of cyanobacteria and other microrganisms with fluorescent DNA/RNA probes
i)	Autofluorescent enumeration	Picoplankton identification and enumeration
j)	Chromatographic methods (HPLC, G.C., L.C.)	Quantification of pigments, amino acids, pollutants, hydrocarbons, and lipids
k)	Stable isotope techniques	Tracing fates and origins of nutrients and carbon sources.
l)	Microelectrode techniques	Identifying microscale chemical gradients, e.g., determining oxygen production and consumption rates characteristic of microzones
m)	Phylogenetic Analysis of Natural Microbial Populations by Ribosomal RNA Cloning and Sequencing	

Recent advances in methodology have made it possible to analyze natural microbial populations phylogenetically by direct cloning and sequencing of rRNA genes from the resident organisms. Thus, for the first time, it is possible to assess the diversity of microbial ecosystems without the biases introduced by the need to cultivate the organisms. The importance of such an approach is underscored by the fact that direct counts and plate counts of microbes often differ by several orders of magnitude when done for most ecosystems.

It would be appropriate to analyze both planktonic and benthic communities by these new approaches. A knowledge of the dominant species present in these communities, aside from its intrinsic interest, would facilitate interpretation of other forms of data, such as those relating to nutrient cycling. Organism-specific DNA probes, complementary to rRNA, will make it possible to count specific microorganisms in numerous samples. Once probes are available, their use is readily implemented in the field.

A4. DRAINAGE BASIN INFLUENCES

IMPORTANCE OF DRAINAGE BASIN INFLUENCES

The flux of nutrients from drainage basins to large lakes is essentially unidirectional. Runoff occurs from both point and non-point sources, and relationships exist between fluvial loadings and concentrations of N, P, Si, and metals. Hydrology varies with season and between years; the timing of major runoff events can influence seasonal progressions and productivity of the receiving waters. Groundwater inputs to large lakes have rarely been studied, but nutrient levels in groundwaters may be high and the inputs may be important.

Water level fluctuations produce a variety of effects on littoral zones. Many large mobile species use littoral or nearshore zones during their life cycles, and the fluctuations alter the habitat characteristics.

DOMINANT RESEARCH CHALLENGES

Mass Balance

Information for input-output budgets of specific nutrients for all of the Laurentian Great Lakes is lacking, notwithstanding the massive data base compiled by the Environmental Protection Agency (EPA). Existing data are of variable quality and availability. For example, EPA methods are suspect with respect to particulate nitrogen and phosphorus; high detection limits are often used and thus values below detection limits are often misused or overlooked in budget calculations. Further, the proportions of N and P which are biologically available are seldom considered; this is crucial when dealing with N and P associated with particulate matter. Airshed inputs are often not measured or are based on few monitoring sites.

Geomorphic Influences

The degree of interaction between the watershed and the lake depends upon the geomorphology of the lake. This coupling can be examined where there is a wide divergence in lake renewal times, or where there are radical differences in shoreline:volume ratios.

Climate and geology are templates upon which most biological, chemical, and physical processes develop. If these relationships can be understood over widely separated geographical settings then it may be possible to predict relationships between solutes in runoff and basin lithologies from climate, soils, and vegetation. From the nutrient loadings, it may prove possible to predict some aspects of the biological communities, especially among the algae.

Runoff Events

Timing and magnitudes of runoff events influence lake communities and processes through several means. A significant riverine input occurring at minimum stability could have a substantial immediate impact on the pelagic region, whereas that same input during thermal stratification would have lesser, and delayed, influence. Advection, convection, magnitudes of fetch, and heat absorption by suspended sediment loads may, in many cases,

be driven by watershed and airshed influences. Timing of runoff events is critical, because communities may have adjusted evolutionarily to the average within-year timing of these events.

Stability of Large Lakes

Great lakes are potentially the most stable limnological systems, but they are certainly not immune from watershed influences. Littoral and riverine processes are important even in large lakes, because most fish species spend part of their life cycle in those zones. The littoral and pelagic environments of large lakes are inherently dynamic and interactive hydrologically and biologically over both the short and long term.

Spatial Heterogeneity

Interactions among watershed processes, hydrodynamic variations, and lake geomorphometry promote a dynamic mosaic of resource patches and gradients. For example, an overflow plume from a tributary river may create a resource gradient or patch continuum over a significant portion of the lake surface. Stochastic weather events can add a further level of complexity. Boundary dynamics between resource patches or along resource gradients may affect community structure and production. Gradients in temperature, light, and nutrients occur across these resource patches and thus they present natural experiments for examining community structure (e.g., Si and P competition among diatom species). Geomorphic gradients and boundaries also may determine the position of the thermocline, euphotic zone, turbidity plumes, nutrient availability, and relative amounts of wetland and littoral areas.

Riverine Inputs and Groundwater Hydrology

Research is needed on pristine tributaries of large lakes and on groundwater hydrology. Undisturbed rivers are probably in equilibrium with local geologies, and the runoff characteristics and chemistries provide valuable baseline data. The role of groundwater inputs to large lakes is virtually unknown. Inputs from mineral springs may be especially important in some cases. Moreover, groundwaters may be primary water and nutrient sources for large scale wetlands, which are important components of many large lake ecosystems.

EMERGING TOOLS, TECHNIQUES, AND FACILITIES APPLICABLE TO GREAT LAKES RESEARCH

1. Experts in physical limnology and great lakes groundwater hydrology must be sought or trained because expertise is lacking at present.

2. Remote sensing can be exploited to collect watershed data in concert with in situ lake data. Present needs are for localized real-time data processing and for efficient, up-to-date geographical information systems capable of storing and processing large data sets.

3. One institution should manipulate the majority of the physical data, develop formats for data management, and develop ways to make large, complex data bases easily available to regional scientists. Existing institutions should be used as much as possible; a single "super" center for great lakes studies is undesirable.

A5. WATER CHEMISTRY

IMPORTANCE OF WATER CHEMISTRY

The chemical properties of bodies of water reflect an array of processes. Atmospheric materials enter the water by gas exchange, from precipitation, and from particle fallout. In turn, gases, aerosol particles, and water vapor escape to the atmosphere. Within the water body, materials partition between dissolved and particulate phases and are taken up and released by biota. Stratification of the water column leads to segregation of materials by depth, and advection moves material from one location to others. Sinking particles commonly carry adsorbed substances downward, sometimes to be released into deeper waters by desorption or particle dissolution and sometimes to reach the bottom sediments. Exchange of dissolved materials can occur between the sediments and bottom waters, with resuspension of bottom sediments accelerating the rates of exchange. Benthic organisms influence chemical properties near the sediment-water boundary by mixing the bottom, by creating microenvironments, and by various biochemical processes.

The complexity of these interacting processes often forces researchers to study selected chemical properties or to otherwise simplify their investigative approach. Studies in large lakes enjoy several advantages over oceanic and small lake environments which improve the likelihood of successfully unraveling complex interactions of fundamental significance:

a) Great lakes provide a variety of aquatic chemical systems, having wide ranges of oxygen, pH, salinity, hardness, alkalinity, temperature, and ionic composition.
b) Offshore regions of great lakes are relatively isolated from watershed and littoral processes and are pelagic in character.
c) Lakes are constrained, unlike open, unbounded oceanic systems. A lake can be studied over lengthy periods of time with the confidence that it contains the same body of water.
d) Temperate zone lakes are "reset" annually by turnover and mixing. Such resetting provides opportunities to follow the progress of changes in chemical parameters which accompany the onset, development, and eventual decay of thermal stratification. In contrast, the many great lakes of the African Rift are permanently stratified and offer important comparisons to annually mixed great lakes.
e) Great lakes have higher sedimentation rates than most pelagic oceanic environments and in the Laurentian Great Lakes, at least, sediment accumulation patterns and rates are well known. Higher-resolution records of their past chemical properties can be obtained from geochemical studies of their sediments.
f) The Laurentian Great Lakes provide an opportunity to investigate the effects of sediment resuspension on chemical processes. Data and samples are available from sediment trap arrays deployed regularly since the late 1970s and constitute what must be the most extensive sediment trap information available from any sedimentary basin in the world.

DOMINANT RESEARCH CHALLENGES IN GREAT LAKES LIMNOLOGY

Primary Production Rates

Discrepancies presently exist between alternative methods of measuring productivity rates in natural systems. The true rates of measuring primary production in most aquatic systems are consequently subject to debate and uncertainty. Great lakes provide bounded pelagic systems in which nutrient pathways and uptake kinetics can be followed more easily and accurately than in the open ocean. They consequently offer a medium in which alternative methods of estimation can be compared, and reasons for the discrepancies understood.

Phosphorus Mass Balances

Existing methods for measuring phosphorus concentrations are crude and inaccurate, resulting in poor mass balances for this vitally significant element. Procedures better able to measure the contributions of the various phosphorus species and indicate their roles in biogeochemical cycles need to be developed. Sediment-water interactions as well as water column processes are important elements of this problem. Great lakes are natural laboratories in which to develop and test these procedures, because the mass balance information is urgently needed for these systems.

Sedimentation and Burial of Biogenic Particles

Formation of calcium carbonate particles, amorphous silica, and fecal pellets by organisms results in transfer of material from the upper water column to deeper waters and sediments. These transfers affect a number of biotic and abiotic processes in both freshwater and marine ecosystems. Great lakes provide special opportunities to evaluate the significances of these events and the mechanisms involved in their chemistry. For example, Lake Michigan experiences annual "whitings", or precipitations of calcium carbonate. The calcium carbonate particles constitute 50-90% of the total particle pool during late summer.

Activities of Chemical Species

Absolute concentrations of natural and anthropogenic chemicals do not determine their behavior in waters. Ion pairing, chelation, and other molecular interactions reduce the activities, or effective concentrations. Molecular kinetic processes like partitioning between particulate and dissolved phases, gas exchanges, dissolution of minerals, and uptake and incorporation of substances by biota depend upon activities, not concentrations. Great lakes present wide ranges of chemical characteristics, from the dilute waters of Great Slave Lake or Lake Superior to the saline Dead Sea and Great Salt Lake, or the monimolimnia of Lakes Tanganyika and Malawi. Because the bounded water masses of great lakes are good places to study many kinetic processes, the influence of chemical conditions on the rates will be a necessary and valuable parallel study.

Carbon Biogeochemistry

The formation, cycling, and remineralization of organic matter influences almost all chemical pathways of lakes and oceans. Comparative studies of carbon biogeochemistry are needed over the entire spectrum of aquatic systems. Great lakes are a major target for study because they contain much of the surface fresh water on earth. Molecular and isotopic tracers for some pathways already exist, but they need refinement, and many more tracers are needed. Gas exchanges with the atmosphere monitored by ^3He or SF_6, and diagenesis within sediments measured with novel tracers present immediate challenges.

Geochemical Processes at Interfaces

The air-water interface, mid-water stratifications, and the sediment-water interface are major boundaries where exchanges and partitioning of chemical materials influence biogeochemical cycles. In the constrained, pelagic settings of great lakes, where mass balances can be obtained, these processes can be studied more easily than in more complicated, open boundary systems.

EMERGING TOOLS, TECHNIQUES, AND FACILITIES APPLICABLE TO GREAT LAKES RESEARCH

Remote Measuring Devices

These can be satellite or airborne remote-sensing devices, as well as instrumented buoys with subsurface measurement devices. Physical, biological, geological, and chemical characteristics of water bodies can be measured, either routinely or for selected intervals or events, and the data transmitted to shore. Such devices can reduce reliance on ships for monitoring activities and free the vessels for in situ experimental work.

Poor Weather Sampling Capability

Annual cycles of the Laurentian Great Lakes remain poorly understood because of poor weather conditions during winter and stormy periods. A moored instrumentation platform, or other such stable platform which could be occupied for sampling and experimentation, and which could withstand winter ice flows, would fill this significant gap in the understanding of large lake science.

Master Reference Stations

Several master reference stations should be established in every great lake being studied to enhance compatibility of data from different investigators and to help build records of long-term trends. These stations would become part of each new study of that lake's chemistry.

Standardized Procedures

Data from different analytical schemes and sampling procedures are not always compatible. If reference stations and long-term data are a goal, then compatibility must be ensured. A workshop on analytical procedures should be convened, and working groups should adopt and issue recommendations about standardized procedures. Even as new techniques evolve, a basis must be established for comparing data from studies conducted by different investigators, on different lakes, and at different times.

Large Lake Data Center

The data collected in present and future studies of great lakes have an ensemble value beyond the needs of individual investigators. They ought to be curated and used for research on long-term trends and geographic patterns. Selection and access of data is the problem. Data could be stored by the Ocean Data Center, or some equivalent, as could information about ongoing and planned programs and the availability of specialized equipment and facilities.

Multidisciplinary Research Program

A coordinated, multidisciplinary research program, similar to programs that have successful in marine systems, is called for in great lake systems. Efforts by single investigators and even by single institutions can not be sufficiently comprehensive to assess the many interactive factors controlling and influencing the chemical parameters of great lakes. Information is needed from other disciplines in several areas:

a) Physical limnology - circulation patterns, advection and mixing rates, residence times, offshore transport times, stratification dynamics.
b) Geological processes - sedimentation rates, resuspension rates, mineralogy of sediments, sediment dynamics, depth of sediment mixing.
c) Biological processes - food web structure, bioturbation by benthos, primary production patterns, community compositions, community stability.

The primary initiatives and administrative structures should rest with academic institutions because the goals emphasize novel inquiries. Many routine monitoring activities are justifiably the province of government agencies.

A6. BENTHOS

IMPORTANCE AND ROLES OF BENTHOS

Benthic organisms can affect flows of materials and energy between the benthic and pelagic regions. These fluxes are important in virtually all large lakes. Lacustrine benthic communities furthermore provide valuable theories of the evolution of community structure and function.

Much theory and experimental evidence about competition and predation has come from studies of marine rocky intertidal benthos. Soft bottom benthos offer interesting parallels and intriguing differences. Macrobenthos play a large role in sediment diagenesis. Collaborative studies between benthic biologists and fluid dynamicists have shown strong effects by organisms on erosive flux of cohesive sediments, and few models of sediment-water interactions now ignore benthos.

DOMINANT RESEARCH CHALLENGES

Community Structure and Function

Large lakes can provide a means to evaluate the importance of system age and stability to biotic diversity and function. In 1969, L. Slobodkin and H. Sanders erected the Stability-Time Hypothesis, suggesting that older and more stable systems would be more diverse and that biotic interactions would be different from young and unstable environments. They argued that species diversity in North American and Eurasian great lakes supported their view. Sanders subsequently examined diversity and abundance in marine soft bottoms world-wide. Detailed parallel studies of lake benthos have not been conducted.

In oceanic environments community ages are not easily determined and age often co-varies with stability. In lakes the contribution of age is determinable, and age and stability are more readily separable. Nonetheless, quantifying the stability and the details of biotic interactions in any one lake or part of one lake is laborious. None of the Laurentian Great Lakes are so understood at present; a number of studies and several years will be required. In addition, given the great age and isolation of some of the lakes, the idiosyncratic role of history in contributing different species groups to different lakes will have to be determined, and this will entail some fairly detailed biogeography and evolutionary systematics.

Marine and freshwater macrobenthos communities in sands and muds are quite different taxonomically, but at a functional level, they are comparable. Each has infauna and epifauna of various mobilities. Each has deposit-feeders and suspension feeders, predators, and herbivores. Marine communities generally contain greater relative abundances of large invertebrate epibenthos. The effect of the differences on community function are unknown. It is likely that expected biota-dependent flux rates of nutrients derived from marine studies will be modified in freshwater environments.

Taxonomic efforts and occasional large scale spatial surveys have already provided the outlines of the distribution and abundance of the Laurentian Great Lakes (LGL) macrobenthos. In these lakes there are a few hundred widely distributed species, with relatively few species numerically dominant. The number of cosmopolitan species is about five-fold above the world average. Widespread species differ greatly in relative abundance from site to site. In particular, nearshore areas differ from offshore areas, and all the regions of the bottom where large rivers open to the lake have a distinct faunal composition. The pattern is attributed to different levels of organic supply and disturbance, but the actual mechanisms are not known. "Indicator" species of pollution stress have been identified, but the studies have not proceeded beyond empirical correlation. Research on species distribution could profitably concentrate on issues of ecological concern, like whether the scale of patch size and the nature of patch boundaries influence the intensity of community interactions, or whether distributions arise primarily through abiotic controls.

Little is known about benthic community function. Many species are morphologically identical and functionally similar (e.g., tubificid oligochaetes) and their coexistence invites explanation. The relative importance of predation and competition for resources deserves high priority in research. The differing abundances and distributions of predatory demersal fish in the upper and lower LGL permit inter-lake comparison studies. Natural and anthropogenic bottom disturbances produce significant mortality in soft bottom communities. Recovery from such disturbances seems to follow a successional sequence. Small scale temporal bottom disturbance could create a time-varying spatial mosaic on the bottom. This relationship may explain why researchers often find significant correlation of benthos distribution and measured physical-chemical variables only in deep, possibly less disturbed water.

Studies in the LGL and elsewhere have shown that macrobenthos modify their habitat and can alter the rates at which biogeochemical processes occur. Strong local interactions, some mutualistic and some antagonistic, are probably involved. The organisms live near a major interface in the region of strong environmental gradients and are large relative to the scale of the gradients; at the same time, the sediment prevents or diminishes far field effects. R. Brinkhurst performed a provocative experiment in 1971 demonstrating that 3 species of oligochates grew faster and respired less in mixed than pure culture, suggesting some sort of mutualism among them. The possibility exists that this could be an excellent environment to test controversial ideas of group selection and true community evolution.

The role and identity of meiofauna in community function ought to be examined. Evidence mounts from marine soft bottoms that meiofauna play a critical role in detritivore communities. They enhance microbial activity and organic matter decomposition and are both the food and predators of macrobenthos. Interrogations of detritus-based food webs are now yielding to some innovative techniques in microbial ecology and organic geochemistry.

Finally, there are some unique habitats whose study is recommended. The first are hardground "reefs" in LGL. Natural outcrops of 2 to 3 m relief, as well as larger artificial reefs exist. They have a distinct fauna and lend themselves to island biogeographic analyses. Is the fauna heavily predated? Do fish seek reefs for food or protection? Is this small but distinctive habitat important to benthic-pelagic coupling?

The second habitat is the bottom of Lake Superior at depths greater than 200 m. Recent submersible activity has changed views of benthic activity. The picture is now one of striking biogenically produced topography densely populated by active benthos. Amphipods burrow, mysids migrate, and sculpins nest and feed with great intensity. Burbots construct fish traps on the bottom for sculpins. Not only do the observations inject a new vitality to views of benthos, but they illustrate benthic-pelagic interactions in a deep lake and the utility of submersibles in great lakes.

<u>Benthic-Pelagic Coupling</u>

The benthic region can be important to the balance and flux of materials in the pelagic zone. Nutrients released from sediments may be redistributed to the entire lake during overturn, or they may be injected upward episodically at metalimnetic instabilities. Benthic-pelagic coupling occurs via remineralization and recycling of organic matter from bottom sediments. In offshore regions of large lakes perhaps 90% or more of the autochthonous organic matter is recycled. The amount of flux owing to material returned from the sediment is unknown, but it may be half or more of the total.

Large macrobenthos, like the suspension feeding unionid clams of the lower Laurentian Great Lakes, can enforce benthic-pelagic coupling through biological means. Unionids dominate the benthos in the western basin of Lake Erie and are even more abundant in Lake St. Clair. Unionids filter large volumes of water and can capture particles on the order of 1 μm. Estimates suggest that they could filter a water volume equivalent to Lake St. Clair in a matter of days. Lake St. Clair may constitute a large natural chemostat, with controlled flow through a small inlet and outlet that can be assayed for nutrients and sediment particles and a growing stable population inside. Analogously, the suspension-feeding clams of San Francisco Bay may cycle daily an amount of water equal to the entire volume of the bay.

Macrobenthos can act as regulators at the sediment-water interface, altering the rates at which material exits the bottom and influencing the manner in which material is preserved. Laboratory experiments indicate that unionids and oligochaetes enhance remineralization via several mechanisms:

a) excretion
b) physical alteration of the bottom
c) enhanced diffusion rates
d) enhanced sediment microbial activity

Nutrients may also leave the bottom in particulate form. Feeding activity of these same organisms can enhance the erosion rate of silt and clay sediments by factors of 2 to 50 at low bottom shear stress. Transport processes include diffusion, macrobenthic advection, current mixing, and bubble ebuliation, but their relative importances in different environments are unknown. In particular, the nutrient fluxes mediated by bacterial metabolism in comparison to macroinvertebrates are unknown.

Benthic-pelagic coupling also occurs via food web interactions. Predation rates by fish on macrobenthos are not known for any great lake. Such community interactions are of great interest because it is the benthic species that show greatest speciation in most ancient great lakes. Transport of materials by vertical migration is also potentially significant, and deserves more attention.

Sedimentary Processes

It is becoming clear that cohesive sediment transport is controlled by macrobenthos and bacteria, but only at low bottom shear stress. The relative importance of large rare storms versus more frequent smaller events is not well known. Macrobenthos mix sediments in fairly well known ways, and they exert a strong control on the resolution and interpretation of paleolimnological signals. Many experimental methods and models developed for the study of mixing by LGL researchers are of great potential value to paleolimnologists.

EMERGING TOOLS, TECHNIQUES, AND FACILITIES APPLICABLE TO GREAT LAKES RESEARCH

Remotely Operated Vehicles

These should be evaluated as a cost effective way to survey areas of the bottom.

Sediment-Water Interface Profile Cameras

These may be a useful rapid survey tool in great lakes.

Ship-Towed Near Bottom Heat or Micro-Motion Detectors

This new technology offers a way to obtain an integrated measure of benthic activity rapidly over large areas of the bottom, and could have an effect analogous to that which remote satellite sensing has had on the study of surface processes.

Molecular and Biochemical Technology

At present the immature stages of most benthos defy identification and few species-specific processes can thus be studied. Any technique that can solve the problem of identifying difficult life stages (eggs, larvae, juveniles) could advance understanding of a variety of species, both freshwater and marine. Monoclonal antibodies and genetic probes utilizing ribosomal RNA hold promising potential.

Benthic Flux Chambers

Remote sampling techniques using benthic monitoring stations moored in situ have great potential for generating long-term standardized data.

Reference Stations and Monitoring

Long-term, semi-annual sampling of a few reference stations would assist the detection of long-term variability and assist monitoring for changes.

Multidisciplinary Consortia

Most of the research problems in benthic environments cover more disciplines than are commonly located at one institution. A formal means of fostering joint studies is desirable.

A7. PALEOLIMNOLOGY

IMPORTANCE AND ROLES OF PALEOLIMNOLOGY

Paleolimnology provides data at four very different time scales which are useful for comparative purposes.

On an annual scale, inputs derived from biological, authigenic, and physical processes can be linked with modern sedimentation rates.

On a scale of decades, records of inputs and losses can be resolved in the sediment record. These records include those for toxic organics, major and trace elements, nutrients, and biogenic components. The biogenic materials provide evidence for coupling between biological processes in the water column and geochemical processes in the sediments.

On time scales of decades to millennia, the 10,000-year record in common among large lakes in North America and ancient lakes in Africa and Asia can be used to study long-term natural variation resulting from changes in global climate.

Ancient lakes offer the longest time scales because they contain sediment records of over ten million years. These lakes have high sedimentation rates which resolve events on scales of years or decades, even at those great ages. These lakes provide an exciting opportunity to study climatic change and evolution of lacustine systems with detail that cannot be duplicated in marine systems.

Paleolimnological studies necessarily must be multidisciplinary. To take maximum advantage of the opportunities requires a coordinated effort among a group with biological, chemical, and physical interests and with several specialties among each discipline. Studies must be integrated with other disciplines working on climate, hydrology, atmospheric transport, and terrestrial vegetation.

Interpretation of lake sediment records requires understanding of linkages between the analytical elements (diatoms, sediment properties, etc.) and the limnological processes responsible for their production, accumulation, and preservation. Adjunct investigations must establish what factors contribute to the formation of a permanent sediment record and resolution of events in the record. These include the sedimentation of biogenic components like microfossils and organic compounds, detrital components derived from aeolian and riverine sources, and sedimentation of authigenic components like calcite and clays. Successful interpretations require knowledge of how physical, chemical, and biological processes affect deposition of materials in great lakes.

DOMINANT RESEARCH CHALLENGES

Lacustrine Evolution

Obtaining long cores from ancient lakes deserves highest priority. These lakes have varying degrees of endemism and speciation and permit high resolution of historical records in their basins, which provides a unique association of circumstances. Lake Baikal and African great lakes may be the temperate and tropical analogs of polar ice cores, with high resolution and the continuous depositional record required to understand global climates.

The Deep Sea Drilling Project has demonstrated the technical feasibility of this endeavor. We recommend Ocean Sciences and other interested divisions of NSF consider the feasibility of sponsoring such an effort perhaps in cooperation with the oil industry which is currently contemplating exploratory drilling of the African lakes.

High Resolution Records of Continental Climate

Data are needed to test models of paleo-climate derived from oceanic sediments. Lake sediments permit resolution of events on scales of years to centuries. Great lakes are in intimate contact with terrestrial systems where the effects of climatic changes are of primary interest to man. These mesoscale basins integrate effects over large areas and are ideal systems to look for global signals including atmospheric input and anthropogenic changes.

Sediment Burial Terms for Mass Balance Studies

These are particularly important in evaluating inputs of anthropogenic compounds and the importance of sediments as material sinks. The best way to obtain information on such linkages is through a combined lake monitoring and sediment trapping research program that runs minimally for 5 years and preferably longer. Periodic and episodic limnological events, like overturn, storms, and whitings should be correlated to the resultant lake sediment record retained in automated sediment traps deployed at sites of suitable sediment accumulation rates.

Lake monitoring must include extra-basin data on climate, hydrology, and relevant watershed characteristics if paleolimnological interpretations are to be extended to environments away from the lake.

Paleolimnology has great advantage in comparing lakes of different sizes with respect to their inherent variability and resilience to external environmental forcing. Analyses of cores from smaller lakes adjacent to great lakes can provide information for such comparisons, and can help interpret sediment records from great lakes that may have muted responses to local environmental impacts.

EMERGING TOOLS, TECHNIQUES, AND FACILITIES APPLICABLE TO GREAT LAKES RESEARCH

Little is needed in the way of new technological developments, but recent innovations in oceanographic instrumentation must be introduced to work on the great lakes. These items should be made available through a shared-use pool to NSF-funded groups.

Sediment Traps

Long-term moorings with time sequential sampling to link neolimnology and paleolimnology.

Side-Scan and Multi-Beam SONAR Systems

Analogous to Sea Mark and Sea Beam for high-resolution analysis of lake-floor morphology, to delineate sediment transport pathways, vents and springs, etc.

Low Disturbance Core Samplers

For detailed study of sediment-water interface processes and early diagenesis.

Standard (Kullenburg) Piston Corer with winches and cable.

Box Corers

These provide large volume samples required for parallel analyses of micro- and macro-fossils, like fish scales and remains.

High-Resolution Seismic Profiler

This must be used to identify sites most suitable for deep drilling.

Deep Drilling System

A feasibility study will be required to determine which ancient lakes offer the best potential records. Lakes Malawi and Tanganyika are promising and have been surveyed by multi-channel seismic reflection profiling. Lake Baikal offers a good, high-latitude contrast. It is also unclear without study whether to construct a relatively mobile system that could be moved from lake to lake or to custom build a rig at each lake we intend to drill. Expertise from the NSF Ocean Drilling Program should be borrowed to address such issues as anchoring vs dynamic positioning, blow-out protection, and overall cost. International cooperation will surely be required.

Core Library

Dating and Magnetic Laboratories

These must be available to provide rigorous dating and stratigraphic control for comparing records among lakes.

A8. BIOCHEMICAL LIMNOLOGY

IMPORTANCE OF BIOCHEMICAL LIMNOLOGY

Limnological phenomena in large lakes can be fruitfully extended to the biochemical level. Mechanisms controlling nutrient dynamics, primary and secondary productivity, and other fundamentally important biotic and abiotic phenomena share a biochemical basis. Advances in molecular biology, physiology, and biochemistry now make it possible to examine regulatory mechanisms which proscribe aquatic metabolism and to tackle ecological and evolutionary questions with powerful techniques and a high degree of sophistication. Many of these techniques and approaches are novel to limnology, and will require development to integrate the technology.

Molecular and biochemical methods are tools which, when used in an ecophysiological context, can yield a wealth of information on large lakes. This field has been hampered in the past by the lack of solid mechanistic theory. Cells have evolved an elaborate, sophisticated set of mechanisms at the cell surface and intracellularly, to deal with changing environmental conditions. Surface receptors enable the cell to sense the chemical environment and evoke the appropriate metabolic response. Methodological constraints and the complexity of natural organismal assemblages have made unequivocal demonstration of such regulation in situ difficult to achieve.

DOMINANT RESEARCH CHALLENGES IN GREAT LAKES LIMNOLOGY

The major areas of research can be divided into a number of categories, some of which represent purely biotically-mediated processes, and some in which biotics and abiotic interactions occur.

Microbial Metabolism

Little is known about the microflora involved in detrital energy flow and nutrient recycling, either in the pelagic, the sediment-water and air-water interphases, or other habitats of great lakes. Several new techniques, including RNA sequencing analysis, are currently being used to identify key species of microflora and picoplankton. These efforts should be expanded to elucidate the structure of microflora communities and their role in energy and materials processing.

This area of research runs the risk of uncritical application of microbial methods to natural communities. The ^{3}H-thymidine uptake technique, for example, although widely used to measure bacterial secondary production, is highly specific for bacterial versus cyanophyte uptake, but it requires extensive evaluation of conversion values for organic carbon synthesis. New technical methodology developed for use on laboratory systems should be extensively and critically evaluated when used to examine the dynamics of natural microbial assemblages.

Molecular Techniques as Evolutionary Tools

The great lakes of the world range from the very old to the relatively young, and from species-rich to species-poor. Considerable research effort should be directed to the use of modern molecular techniques as tools to examine evolutionary questions in these lakes. Electrophoretic techniques,

DNA hybridization, and other molecular approaches are being developed to examine the evolution and phylogeny of unicellular and multicellular organisms. Great lakes are ideal systems to examine speciation dynamics and population genetic variability within or among lakes. Such techniques are already being applied to Daphnia hybridization in other lakes.

Nutrient Dynamics

Despite an apparent wealth of information on nitrogen, phosphorus, and carbon dynamics in large lakes, many fundamental questions about nutrient dynamics remain unanswered. Correlation analyses, while useful as tools, do not explain why these relationships exist, their underlying mechanisms, or the degree to which organisms are able to vary their responses to nutrient stress.

For example, the role of light versus nutrient limitations in constraining planktonic primary productivity in great lakes of varying depth is one of the major questions posed by Fee and Hecky (Appendix B1). To answer this question requires comprehensive knowledge of the relative ability of plankton to utilize all available P, N, and C forms, particularly organic P, N, and C, plus metals required for algal metabolism. The total quantity of N, P, and C present in the water is important, but not as important as the availability of these elements as nutrients.

The major biologically available forms of P, N, and other compounds should be investigated by more sophisticated techniques than chemical hydrolytic assays. Current models of P and N dynamics in the epilimnion do not adequately treat the interactions between nutrient availability, uptake and release by plankton, and sequestering or release of P and N compounds via abiotic, surface-active phenomena (e.g., humic acid-iron-P complexes, adsorption and release from $CaCO_3$-matter complexes, etc). Techniques which address such analytical-kinetic questions include column chromatography, especially new fast affinity matrices to which investigators can attach their own operator-defined ligands, density-gradient centrifugation, and other rapid-separation techniques commonly used by cell biologists.

New questions can be posed about nutrient dynamic properties of great lakes. What scale effects distinguish biotic from abiotic cycling of P in large lake systems versus smaller basins? If large lakes are isolated from their watersheds, and if dissolved humic material inputs to large lakes are high (as in Lake Superior), humic-P sequestered in the open waters could influence pelagic P recycling in a major way. The "whiting" phenomenon in Lake Michigan, for instance, may be alterable if humics inhibit nucleation of $CaCO_3$ and concomitant sorption of P to $CaCO_3$.

Further challenges attend the chemical and biotic processes at interphases (e.g., sediment-water, air-water, etc.) and the regulatory compounds (e.g., hormones, nucleotide derivatives, etc.) potentially present in the DOC/DON pool of lake water. Efforts to characterize compounds in the great lakes are encouraged, not only because they are potential sources of carbon, phosphorus, and nitrogen, but they are also soluble metabolic regulators.

Chemical Communication and Metabolic Coupling Between Organisms

Compounds released by one group of organisms sometimes affect the biology of other, taxonomically distinct groups by allelopathy or other means. The presence of endogenous compounds like a-tocopherol in prey can markedly influence the biology of predatory organisms. At present, our knowledge of the effect of compounds released by algae, bacteria, zooplankton, and fish on other organisms is virtually nonexistent. Biologically active compounds such as cyclic nucleotides are present in lake water, and these compounds are actively released by algae, bacteria, and zooplankton in seasonally and diurnally varying rates. Great lakes are ideal systems to study pelagic or benthic interactions, without major interference from littoral or allochthonous inputs. New methods for the isolation of bioactive organic compounds, especially column chromatography, will be required.

Genetic Engineering

Only one effort is in progress to alter the biology of a Laurentian Great Lakes organism via "biotechnological" means; this is a project to increase the size of game fish in Minnesota via manipulation of growth hormone levels. Potential future implications of genetically engineered organisms in Great Lakes systems include attempts to clone genes for the expression of nitrogen fixation capacity from N-fixing prokaryotes to other unicellular algae.

EMERGING TOOLS, TECHNIQUES, AND FACILITIES APPLICABLE TO GREAT LAKES RESEARCH

Specific recommendations for expansion of biochemical research on Great Lakes systems (1) take advantage of the utility of the Great Lakes in illustrating globally important freshwater problems, and (2) use the institutional expertise already concentrated at institutions in the environs of the Laurentian Great Lakes. Interdisciplinary interaction between biochemists and limnologists can provide the needed expertise to address biochemical/ecological questions with proper encouragement:

1. Major research institutions should hire personnel trained in molecular/biochemical techniques, who wish to cross-over into limnological research.
2. Students and postdoctoral researchers must be trained in modern analytical techniques, so that they can use them in their own research. Institutionally, we must foster cross-disciplinary research. Difficulties beset what reviewers and granting agencies feel is speculative research, with a higher than normal chance of failure. Greater efforts must be expended to enhance funding for cross-disciplinary research.
3. NSF should consider an exploratory grants program consisting of relatively small (e.g., 20-30 K) grants for investigators wishing to do the innovative "first question" research demanded by our limited background in biochemical limnology.
4. A meeting between limnologists and interested physiologists, biochemists, and molecular biologists is desirable. The goal of this workshop would be two-fold. First, limnological investigators could adapt new techniques to lake studies. Second, new researchers may enter the field who had not worked on aquatic systems, but who might recognize the utility of great lakes for their own research programs.

A9. PHYSICS AND REMOTE SENSING

INTRODUCTION

For the most part, these disciplines can proceed independently of non-physical disciplines. However, selection of suitable problems and subsequent reporting of findings must be guided by the needs of a multidisciplinary, ecosystem approach.

Temptations to collect vast data sets of ever-increasing spatial and temporal resolution must be tempered by realistic assessment of the human energy available for analysis and the need to deliver information without excessive delay. Data collections should be biased to long data sets; simple repeated observations are preferred over complicated single efforts. Coordinated planning, execution, analysis, and reporting of experiments is essential. Most undertakings are beyond the capabilities of single institutions.

RESEARCH CHALLENGES IN GREAT LAKES LIMNOLOGY

Basin Scale Horizontal Circulation

a) Time Scales:
- Storm events (2-3 days)
- Natural periods of basins (5-10 days)
- Seasonal
- Flushing times
- Mixing times

b) Space Scales:
- Basin widths (100 km)
- Basin depths (100 m)
- Mixed layer depths (10 m)

c) Topics:
- Properties of horizontal distributions governed by the "conveyer belt" effect; for instance, the fate of the Niagara River plume in Lake Ontario.
- Differences between stratified and unstratified basins.

d) Tools Needed:
- Current meters accurate in 1 cm/s range with long immersion life.
- Expanded fleets of satellite and LORAN tracked drogues carrying sensors for wind speed, surface temperature, and other properties.
- New tracer techniques, including possibly SF_6.
- Synoptic, remotely sensed "pictures" of surface temperature and turbidity, as often as daily.
- Expansion of satellite transmitted data from buoys.
- Survey aircraft for the Laurentian Great Lakes.
- Hydrodynamic models coupled with data have led to increased understanding of essential dynamics, and tool should be used repeatedly.

Small Scale Horizontal Circulation; Nearshore/Open Lake Exchanges

a) Time Scales:
Storm cycles
Natural period of basins
Lifetime of small scale features (hours)

b) Space Scales:
10-20 km offshore
10 km alongshore

c) Topics:
Mixing and transport of river and outfall plumes.
Land runoff and recently eroded sediments.
Coastal residence time in relation to biogeochemical cycles.
Springtime nearshore thermal fronts.
Upwelling.
Oceanic and lake coastal boundary layers appear similar from coastal zone color scanner, with squirts, jets, and filaments evident. What is the relation of these surface features to onshore/offshore exchanges?
High water levels and accelerated erosion.

d) Tools Needed:
Current meters that work in the wave zone and in waters with high sediment concentrations.
Fast transecting hovercraft or aircraft.
Daily remote sensing data in spatial resolution of approximately 100 m.
Telemetering devices.
Models to develop and test parameterization of mixing processes in order to permit incorporation of non-physical processes.

Vertical Processes and Vertical Structure

a) Time Scales:
Turbulence (seconds)
Seasonal

b) Space Scales:
Fine structure of turbulence (1 cm)
Depth influence of waves (100 m)

c) Topics:
Light penetration and optical properties related to biological activity and absorption of radiant energy
Distribution of turbulent mixing as governed by buoyancy and heat flux, and mean current shear.
Distribution of both acoustic and optical scatterers both as tracers of physical processes and for biological purposes.

d) Tools Needed:
Profiling devices and roving devices carrying current meters, D.O. probes, fluorometers, spectrometers, and conductivity sensors.
Acoustic profiling devices to measure velocities and particle distributions.

Experiment designs that can detect the difference between horizontal advection and time changes in vertical distributions.
Airborne LIDAR is a potentially useful mapping tool that could fill in the gaps in horizontal arrays of fixed instruments.
Models are essential to test parameterizations of turbulent mixing, a crucial interface between biology and physics.

<u>Sediment Processes: Resuspension, Nepheloid Layers, Transport</u>

a) Time Scales: Residence times of particulates in water column (seconds to seasonal)

b) Space Scales: Nepheloid layers (10-50 m)
Sediment resuspension boundary layer (1 m)

c) Topics: Appearance of nepheloid layers in low energy environments; conditions for existence and potential effects on geochemistry.
Episodic resuspension in high energy environments under steady flow from currents or oscillating flow from surface waves.

d) Tools Needed: Acoustic equivalents of LIDARs to yield size distributions and concentrations of particles.
Optical techniques like nephelometry, laser scatter detection, underwater LIDAR.
Arrays of small fixed current meters operated at high sampling rates in turbulent wave dominated regimes.
Sediment traps and time lapse photography.
Profiling techniques from Project A9.2.3.
Techniques borrowed from coastal oceanography.

<u>Surface Boundary Processes</u>

a) Time Scales: Direct measurement of turbulent fluxes (fractions of seconds)
Seasonal
Interannual

b) Space Scales: Variation of mean properties (basin scale)

c) Topics: A major uncertainty in numerical circulation models is how to formulate wind stress in terms of mean flow conditions, wind speed, wave conditions, and atmospheric stability. Variations of wind speed across large lakes are not reliably inferred from land data.
Evaluation and models of surface heat fluxes, particularly long-wave radiation from atmospheric data and latent heat flux of evaporation.

Gas exchange models.
Surface waves; large lakes offer a variety of depths and fetches. The best operational wave forecasting models have come out of Great Lakes work.
Importance of wave erosion at high water levels.
Collaborative studies with meteorologists on meso-scale weather effects, the driving force for a major integrated lake study like IFYGL.

d) Tools Needed: More and better meteorological buoys. A standardized Great Lakes design would facilitate assemblage of large fleet, comparable data sets, and economies of purchase.
Remote sensing tools like synthetic aperture radar, to allow effective mapping of the wind stress field.

Lake Ice Effects

a) Time Scales: Hours to Seasonal

b) Space Scales: 10 m to basin

c) Topics: Important effects in Laurentian Great Lakes and lakes in Boreal and Arctic Canada, as well as the Baltic Sea.
Closed nature of basins, large range of sizes, and ease with which areal extent of ice cover can be monitored with aircraft or satellite make large lakes attractive sites, particularly if studies are part of a meso-scale meteorology experiment.

d) Tools Needed: Remote sensing information from aircraft or satellites

Water Quantity Problems: Lake Levels and Diversions

a) Time Scales: Scales of climatic change (seasonal to millenia)

b) Space Scales: Basin and regional

c) Topics: Global issues of water distribution and climate change.

d) Tools Needed: Mapping techniques
Simulation models
Paleolimnology

Natural Pigments as Tracers of Biological Activity

a) Time Scales: Hydrodynamical and biological processes (days to seasonal)

b) Space Scales: 100 m to basinwide

c) Topics: The success of biological indicators like chlorophyll a and its degradation products pheophytin and pheophorbide suggest that more detailed signatures of biological processes can be developed. Until demonstrated otherwise, it is wise to assume that relationships between concentrations, process parameters, and species distributions are system specific. Knowledge of specific properties of pigments is required to deconvolve overlapping spectra.

d) Tools Needed: High pressure liquid chromatography
Whole-cell spectra and techniques that deal with water samples.
Narrow band (10 nm) imagery spectrometers with spatial resolutions of 50 m. These devices will permit large scale mapping of horizontal distributions and evaluation of patchiness.

APPENDIX B1

LIMNOLOGICAL SCALE EFFECTS: PERSPECTIVES ON GREAT LAKES RESEARCH TO THE YEAR 2000

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Great lakes have unique properties that make them ideal sites for studying long temporal and large spatial scales. Indeed, they may prove to be the best environments on the earth for studying global spatial scales and recent geological time scales. That they are uniquely appropriate to the study of global phenomena follows from a hypothesis that states that ecosystem properties are inherently less temporally variable in large lakes than in small ones. If this hypothesis is true, then it follows that it will be easier to detect global signals in data from large lakes than small ones. On the other end of the size spectrum are the oceans: these are certainly big enough to address global questions but in many cases they are not as well suited as great lakes because they are all part of a single interconnected system. The clearly defined boundaries and unidirectional flows of inputs and outputs makes it much easier to obtain accurate balances of materials and energy in great lakes than in the oceans.

DIFFERENCES BETWEEN LARGE AND SMALL LAKES

The question of how aquatic systems change with increasing size is fundamental to the extrapolation of observations and experiments from small lakes to great lakes or from great lakes to the oceans. Because of logistical problems that are involved in performing lake-wide manipulations, multi-year, whole-lake experimental tests of fundamental limnological hypotheses can only be done on small lakes. Results from such experiments have been used to develop management strategies for lakes of all sizes, including great lakes. For example, The hypothesis that phosphorus is the key element in the eutrophication of the Laurentian Great Lakes was verified by whole-lake experiments done at the Experimental Lakes Area (ELA) in Northwestern Ontario (Schindler 1974). Yet the surface areas of the lakes where these experiments were done are only 5 to 25 hectares - ~400,000 to 100,000 times smaller than Lake Ontario. Because we have no theory that will allow us to predict how size per se modifies the manner in which lakes process inputs of materials and energy, it has simply been tacitly assumed that such small lake experimental results are applicable over this incredibly wide range of sizes. Similarly, such extrapolations ignore known relationships between lake size and species diversity, e.g., of the fish community (Eadie and Keast 1984; Rago and Wiener 1986). The role of species diversity in aquatic ecosystems cannot be appreciated from the study of small lakes alone.

We are currently studying how fundamental limnological processes change as lakes increase in size. Our goal is to test the hypothesis that there is little change in ecosystem function over a very broad spectrum of lake sizes. There are, of course, several ways to think about lake "size": a shallow great lake (e.g., Lake Winnipeg, Lake Erie) that rarely or only intermittently stratifies is fundamentally unlike a stratified great lake of similar surface area at the same latitude (e.g., Lake Athabaska, Lake Ontario). Therefore, in order to simplify the subject, we consider only one class of lakes - thermally stratified ones. Within this class, we further simplify by studying lakes in a single physiographic and climatic region. Our study lakes are located in the Red Lake District of the Canadian Shield in Northwestern Ontario - a very remote region about 150 km north of Lake of the Woods. Lakes that we are studying are accessible only by floatplane, and we are reasonably sure that they will remain in this undisturbed state for the proposed period of our study: 10 years. We spent the summer of 1985 surveying the range of lake "sizes" in this district. The 130 lakes that we sampled ranged in surface area from 75 ha (~ 4x the size of a typical ELA lake and 25,000x smaller than Lake Ontario) to 36,000 ha (1,440x larger than an ELA lake and 50x smaller than Lake Ontario). From this size spectrum we chose six lakes for intense study.

We selected lakes for study based on the criteria that they have comparable shapes, maximum depths, and water renewal times. In spite of the fact that they are all in the same geological district, there remains considerable variation in basic water chemistry in these six lakes (dissolved inorganic carbon (DIC) concentrations vary from 150-550 $\mu M \cdot L^{-1}$). Our experimental design implicitly assumes that such differences in ionic strength will not add distracting noise to the signal caused by increasing lake surface areas by over 2.5 orders of magnitude.

Figure 1 shows some of the data that we obtained from these lakes in 1986. Midsummer chlorophyll levels and extinction coefficients were similar in all six lakes, indicating that aggregate phytoplankton abundance and penetration of light were similar in all of these lakes. The other panels of this figure thus show how other limnological variables change as functions of lake size.

There were obvious effects of lake size on water temperature, with smaller lakes heating much faster in the spring and achieving higher midsummer maxima. Because temperature directly affects many important biological rate processes (e.g., respiration, nutrient regeneration, and photosynthesis per unit of chlorophyll at optimum light), such temperature differences could cause important differences in lake function. Consider, for example, the 7C° temperature difference between the smallest and largest lakes at the time of our first observation in the spring. Temperature differences of this magnitude are particularly important at this time of year because this is when nutrient concentrations are highest (due to spring overturn and peaks in surface runoff). Further, solar insolation is near its annual maximum in the spring. All of these factors work together to cause phytoplankton photosynthesis to peak in the spring (Wetzel 1975). This was evident in our larger lakes (Fig. 2), but we apparently began sampling too late to catch this peak in the smaller lakes.

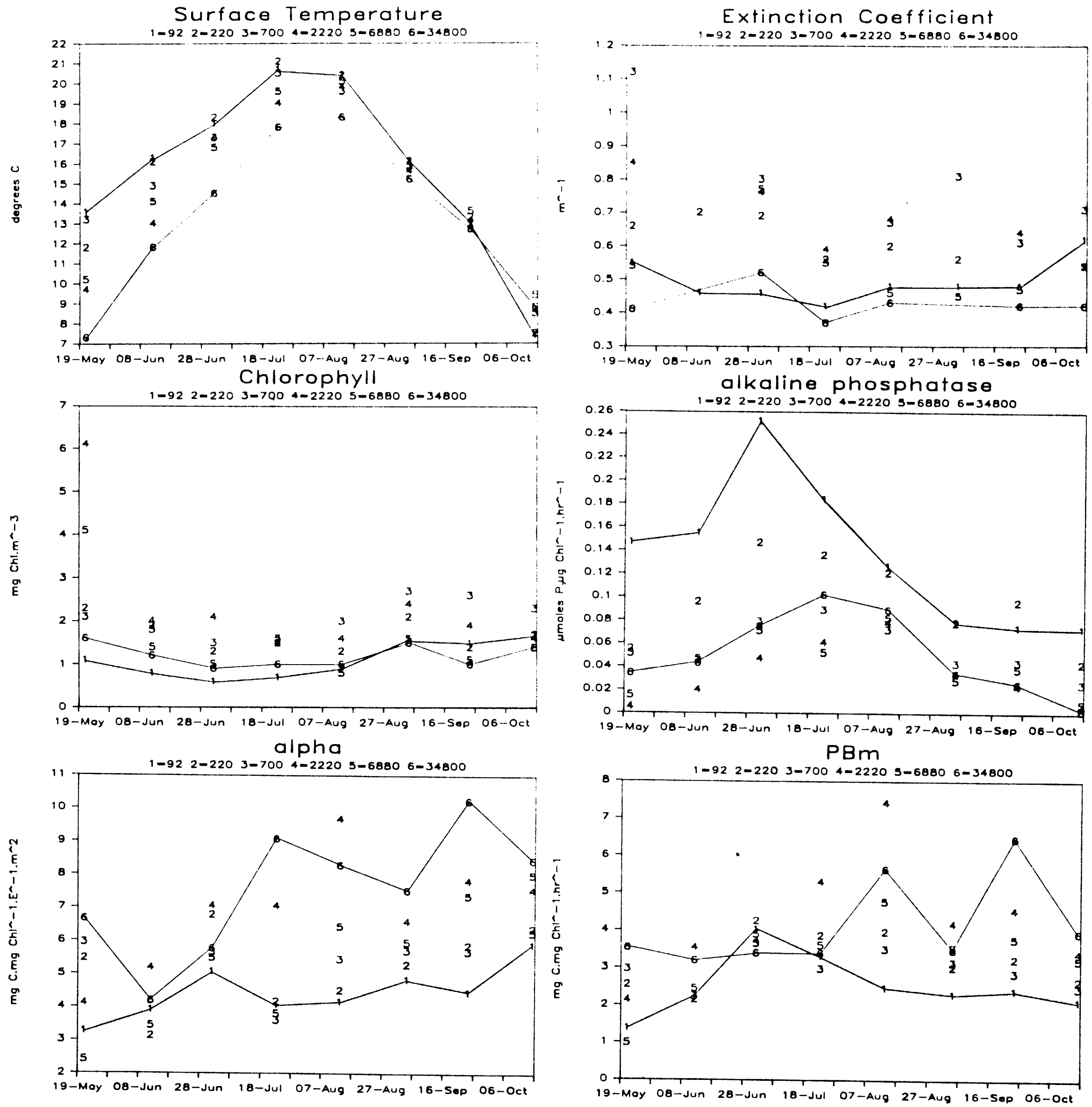

FIG. 1. Seasonal variations of limnological variables in the Red Lake District, northwestern Ontario, during 1986. The values for each of the six lakes are denoted by numbers, with 1 being the smallest lake and 6 being the largest; the areas (in hectares) of the lakes are given at the top of each panel. Data from the smallest and largest lakes are connected with lines.

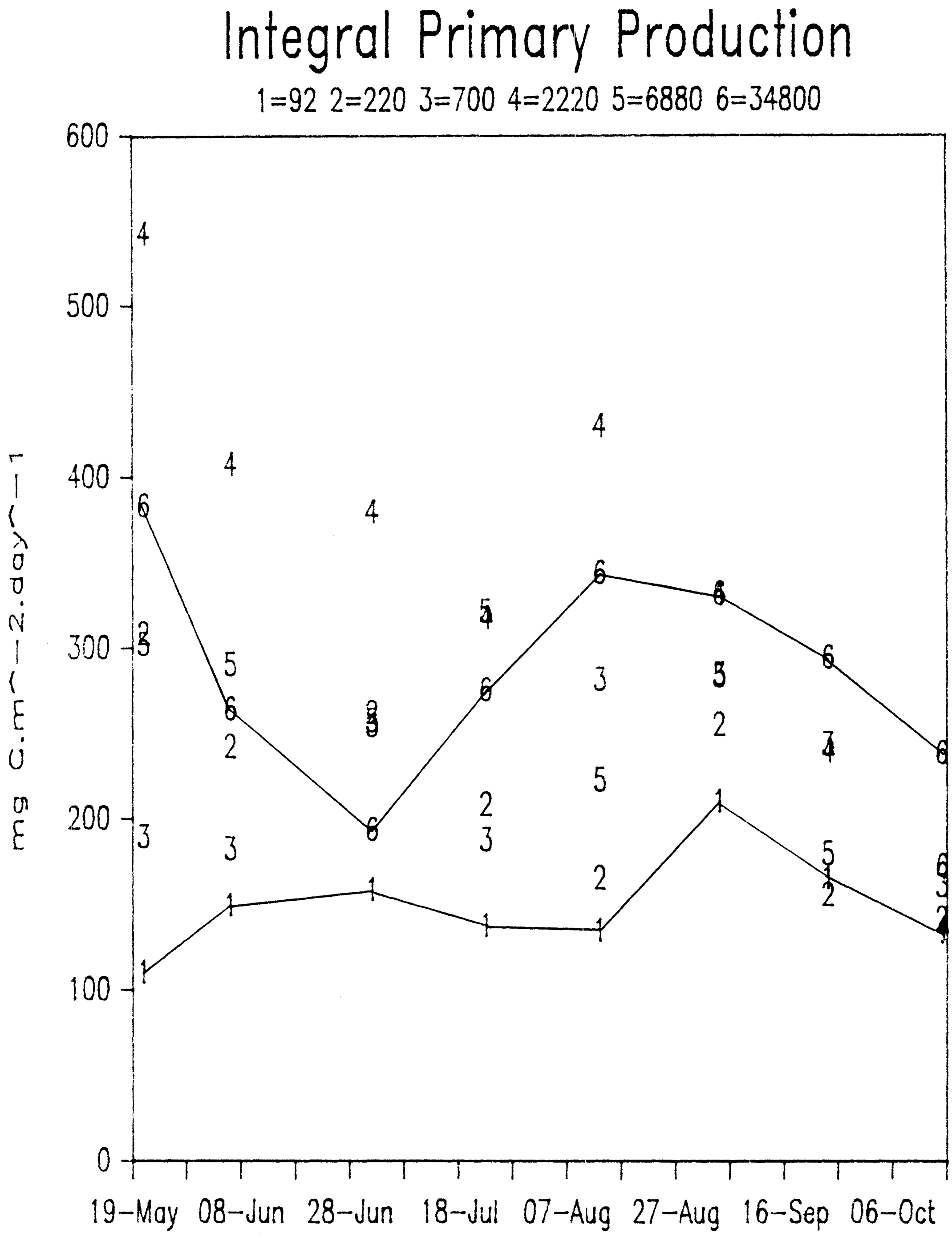

FIG. 2. Seasonal variation in daily integral primary productivity in the Red Lake district in 1986. Annual integrals vary from 26 to 55 $gC \cdot m^{-2} \cdot yr^{-1}$ in lake 1 and lake 4, respectively. See legend to Figure 1 for further details.

One unfortunate consequence of our sampling method is that we were unable to measure temperature profiles in a consistent fashion (because the aircraft could be anchored only in light winds). Nevertheless, it is well known that large lakes have deeper midsummer mixing depths than small lakes. Over the size range that we studied, the midsummer mixing depths should range from ~4 meters to ~15 meters (Patalas 1984). Since transparencies in all of our study lakes are similar (Fig. 1), algae in the large lakes (deeper mixed depths) will experience lower mean light levels. This should cause phytoplankton in large lakes to be more light and less nutrient limited than algae in small lakes (Nalewajko and Voltolina 1986). Our alkaline phosphatase and photosynthesis parameter data support this hypothesis. [Alkaline phosphatase is an indicator of phosphorus deficiency, with higher values indicating a greater degree of phosphorus deficiency (Healey and Hendzel 1979). The photosynthesis parameter (the slope of the photosynthesis vs light curves per unit of chlorophyll) increases when light becomes limiting, while Pm^B (the light saturated rate of photosynthesis per unit of chlorophyll) decreases when nutrients become limiting (Hecky and Guildford 1984)]. Large lakes had consistently lower alkaline phosphatase values (up to three times lower in midsummer) than the small lakes, indicating that phytoplankton in them were much less phosphorus deficient than those in the small lakes. Pm^B was lower in the small lakes, indicating more intense nutrient limitation there. Because differences in chlorophyll concentrations and transparencies in this series of lakes were minor (Fig. 1), we interpret the two-fold difference in annual production, with the smaller lakes being less productive than the larger ones (Fig. 2), as being the net result of these differences in photosynthetic parameters.

Finally, although we have no direct measurements, it is well known (Mortimer 1941-42) that turbulence levels in the thermoclines of large lakes are higher than in the small lakes. If gradients of nutrients are similar, high turbulences cause higher rates of nutrient transport through the thermoclines of the large lakes than small ones. Such transport would further relieve nutrient stresses on algal populations, contributing to the situation that we observed, with phytoplankton being less nutrient limited in larger lakes. High levels of turbulence would also inhibit the buildup of algal populations along thermal or nutrient gradients in big lakes. Consequently, the huge algal "peaks" (300-400 $\mu g \cdot L^{-1}$ of chlorophyll) seen below the mixed layer in small ELA lakes (Fee 1976) cannot develop in larger lakes.

THE CENTRAL HYPOTHESIS

As important as these known differences between large and small lakes are, we believe that the most important difference - the one that makes large lakes uniquely suitable for studying global phenomena - is related to the inherent temporal variability of lakes of different sizes. Large lakes are, we hypothesize, inherently less variable in time than small lakes. We base this hypothesis on the following facts. (1) Water turnover times in small stratified lakes (typically 0.5 to 10 years) are much shorter than

in stratified great lakes (commonly 50 to >100 years). Because of this, changes in inputs of waterborne substances should theoretically affect small lakes more quickly than large ones. (2) As lakes become larger, it becomes less likely that disturbances short of geologic upheaval or climate change will affect the entire drainage system. For example, a forest fire just large enough to consume the drainage basin of a 50 hectare lake would be hardly noticeable in the drainage basin of a great lake. (3) Small lakes chosen for whole lake experiments usually have few or no upstream lakes in their drainage basins. Such lakes are directly affected by runoff from terrestrial ecosystems. On the other hand, virtually all streams that enter a great lake contain waters that have been "processed" by upstream lakes. Upstream lakes retain dissolved and particulate materials, so the temporal variability of waterborne chemical inputs to great lakes should be less than that of small lakes. (4) As lakes become larger, they become less nutrient and more light limited (see above); therefore, natural year-to-year variations of nutrient supply are less likely to induce changes in ecosystem function in great lakes than in small, severely nutrient limited lakes. In short, year-to-year variation of biological properties in great lakes are primarily dependent on internal processes (transparency, internal nutrient recycling) while in small lakes external processes (nutrient loading) are of much greater relative importance.

The hypothesis that large lakes are less variable in time than small ones, which is probably just a special case of a more far-reaching "Ecological Uncertainty Principle," is the key reason for studying global phenomena in great lakes. If it is correct, then only 1-2 years of work might be required on an internally dominated great lake to obtain information on a given global process instead of the decades that would be required to obtain a comparable characterization from a small lake. As an example, consider the year-to-year variability of the biological parameters (α and Pm^B) that must be known in order to be able to convert remotely sensed chlorophyll data into phytoplankton primary production estimates. In small ELA lakes these parameters varied by 300% over an 8-year period (Fig. 3) (Fee et al. 1987). This means that a unit of chlorophyll was responsible for three times as much carbon flow in one year than in another in these small lakes. In lakes with this magnitude of variation, it would be necessary to calibrate each set of remotely sensed chlorophyll data with actual measurements of α and Pm^B in order to obtain reliable estimates of primary production. However, if the "central hypothesis" is true, the year-to-year variability of these parameters would be smaller (hopefully substantially smaller!) in great lakes, and only a few years of study might thus be required to obtain representative parameters' values for different global sites.

Extending our Red Lake series upward to include Lakes Nipigon and Superior, which lie to the immediate east of the Red Lake District, would provide a fairly complete picture of how size per se alters function in mid-latitude stratified lakes. This work alone, however, would clearly be incapable of establishing the applicability of our "central hypothesis" to great lakes located in other climatic regions (e.g., Great Bear Lake, Lake Tanganyika). For example, midsummer maximum surface temperatures ranging

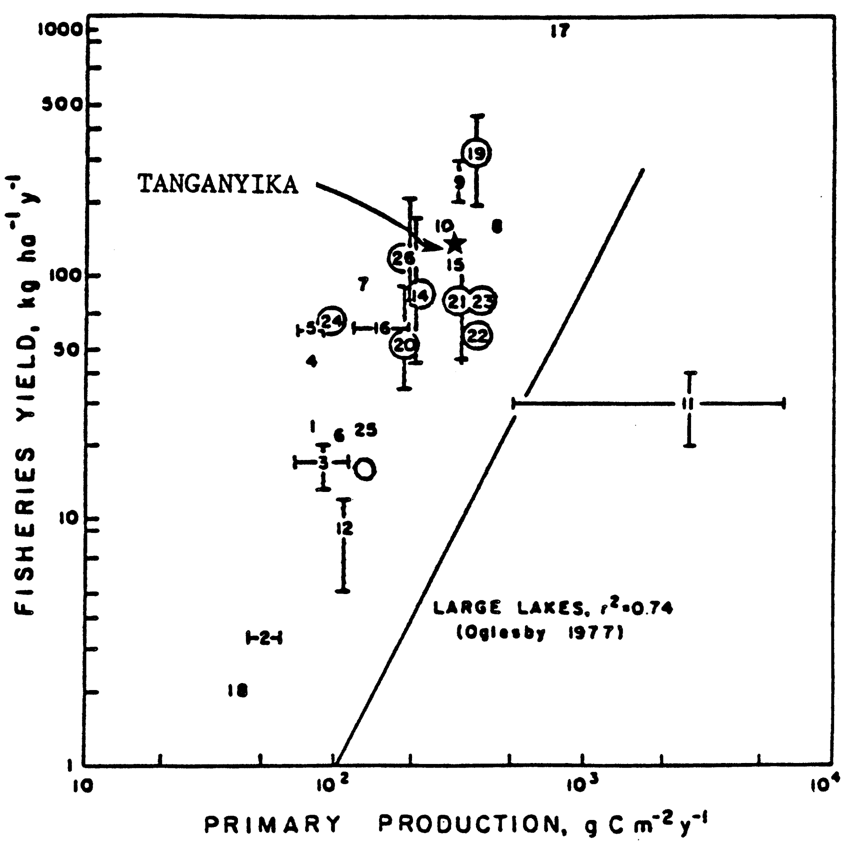

FIG. 3. Fishery yields vs. annual primary production rates (from Nixon and Pilson 1983). Note how similar Lake Tanganyika is to the oceanic systems.

from 4 to 11°C have been observed in Mcleod Bay (an oligotrophic part of Great Slave Lake) in unusually cold and warm summers, respectively (Brunskill 1986). As a consequence, small lakes at this latitude (62°N) that always reach temperatures of - 20°C might show less year-to-year variability that a great lake. Thus, in order to elucidate the global scale, our study needs to integrate with similar ones from subarctic and tropical locations. Such work is clearly required before global productivity estimates can be made from remotely sensed chlorophyll data calibrated with short-term studies on individual lakes. We emphasize that uniform methodologies must be applied for such studies to reach their potential.

If our "central hypothesis" proves to be correct, then a remarkable latitudinal series of great lakes, going all the way from equitorial Africa to subarctic Canada, is available for studying the functional determinants of global productivity. The only previous attempt to study global productivity patterns (the International Biological Program) foundered primarily because it focused on small lakes; local effects and high variances made it difficult to detect interregional (global) differences. The only ocean systems that are comparable to great lakes in size are "cold" and "warm" core rings which are definable water masses but with very limited lifetimes. These are the current rage in biological oceanography because of their bounded nature - something that great lakes limnologists take for granted.

CLIMATE RESEARCH

One of the primary reasons for working on longer time and larger space scales is the relevance of phenomena that operate on these scales to current and proposed research on global climate change. The interaction between large water masses and the atmosphere in different parts of the globe is a critical issue in this work. Because of their large areas the oceans are the main sites of such interactions, but the world's great lakes can and should be used as laboratories to study the processes that are involved. They have the advantages of being large enough to incorporate oceanic-scale processes but they have well defined boundaries and are constrained to specific global locations extending from the tropics to the subarctic. Just as important, the water columns in lakes approach steady-state with local climate whereas in the oceans the deep water in the tropics is polar in origin (Broecker 1982).

Water bodies preserve a unique record of their histories and their watersheds' histories within their sediments. Because lakes have more rapid sedimentation than the oceans, their sedimentary records offer much greater temporal resolution. Questions about the intermediate-term (centuries to millennia) evolution of the atmosphere and hydrosphere (i.e., climate change) can thus perhaps best be approached through paleolimnological studies. It is unclear, however, what "size" of lake is best suited to such investigations; the answer will depend not only on the inherent variability of lakes of different sizes but also on the complications that occur in great lakes due to sediment redistribution (Edgington and Robbins 1973; Lineback and Gross 1972). In any case, the limitations

of this methodology must be established through long-term (decadal), real-time comparisons of observed lake conditions and the forming paleolimnological record. Without such real-time information it will never be possible to fully understand how the patterns preserved in sediments reflect the actual conditions that exist in the overlying water column. Decadal time series of actual limnological conditions in a range of lake sizes at different global locations will provide the basic information needed to interpret the sedimentary record in terms of climate change.

ECOSYSTEM STRUCTURE AND FUNCTION

The world's great lakes are excellent sites for studying the effect of geological time scales on the structure and function of ecosystems. Some great lakes are but a few thousand years old [Great Bear Lake, Great Slave Lake, Lake Winnipeg, Lake George (Uganda), Lake Manitoba] while others (Lake Baikal, Lake Tanganyika, Lake Malawi) are millions of years old. These extremes of age have resulted in extremes of biological community structure. Consider Lake Tanganyika and Lake Malawi: each has hundreds of fish species, most of which are endemic (found nowhere else) (Hecky 1984). Compare this to Great Bear Lake, where there are only 11 fish species, none of which is endemic (Johnson 1975). It would be hard to find sites better suited to determining how biological interactions and ecosystem maturity affect ecosystem function.

One hypothesis of this sort that came out of work on a great lake (Lake Tanganyika: Hecky et al. 1981) is that trophic transfers are more efficient in environments where species richness is high (as it is in the oceans) (Fig. 4). Again, the contrast between Lake Tanganyika and Great Bear Lake is striking: Lake Tanganyika (Coulter 1981) is currently yielding 125 $kg \cdot ha^{-1}$ of fish biomass, which on a whole-lake basis turns out to be an annual catch greater than the entire Canadian Great Lakes commercial fishery. The estimated potential sustainable yield from Lake Tanganyika is greater than the total (freshwater and marine) commercial fishery of Canada, the 12th largest producing nation in the world. Great Bear Lake, on the other hand, yields only 0.3 $kg \cdot ha^{-1}$ (Yaremchuk 1986) and is managed only for trophy sport fish, having been judged unable to support a commercial fishery. The ratio of actual fish yields in these two lakes is >1:400. Assuming that the phytoplankton production of Great Bear Lake is comparable to McLeod Bay (Great Slave Lake), which has a comparable thermal regime and transparency (Fee et al. 1985), this ratio is ~10 times higher than the ratios of annual primary production in these lakes (10 $g \cdot m^{-2}$ in Great Bear Lake vs 365 in Lake Tanganyika; see Hecky et al. 1981 for Lake Tanganyika data). Trophic efficiency is very different in these two great lakes and development of a biologically efficient community such as exists in Lake Tanganyika may take a very long time. However, great uncertainty must be attached to such calculations because the dynamics of the plankton community of Great Bear Lake are unstudied and this calculation requires highly comparable methodology.

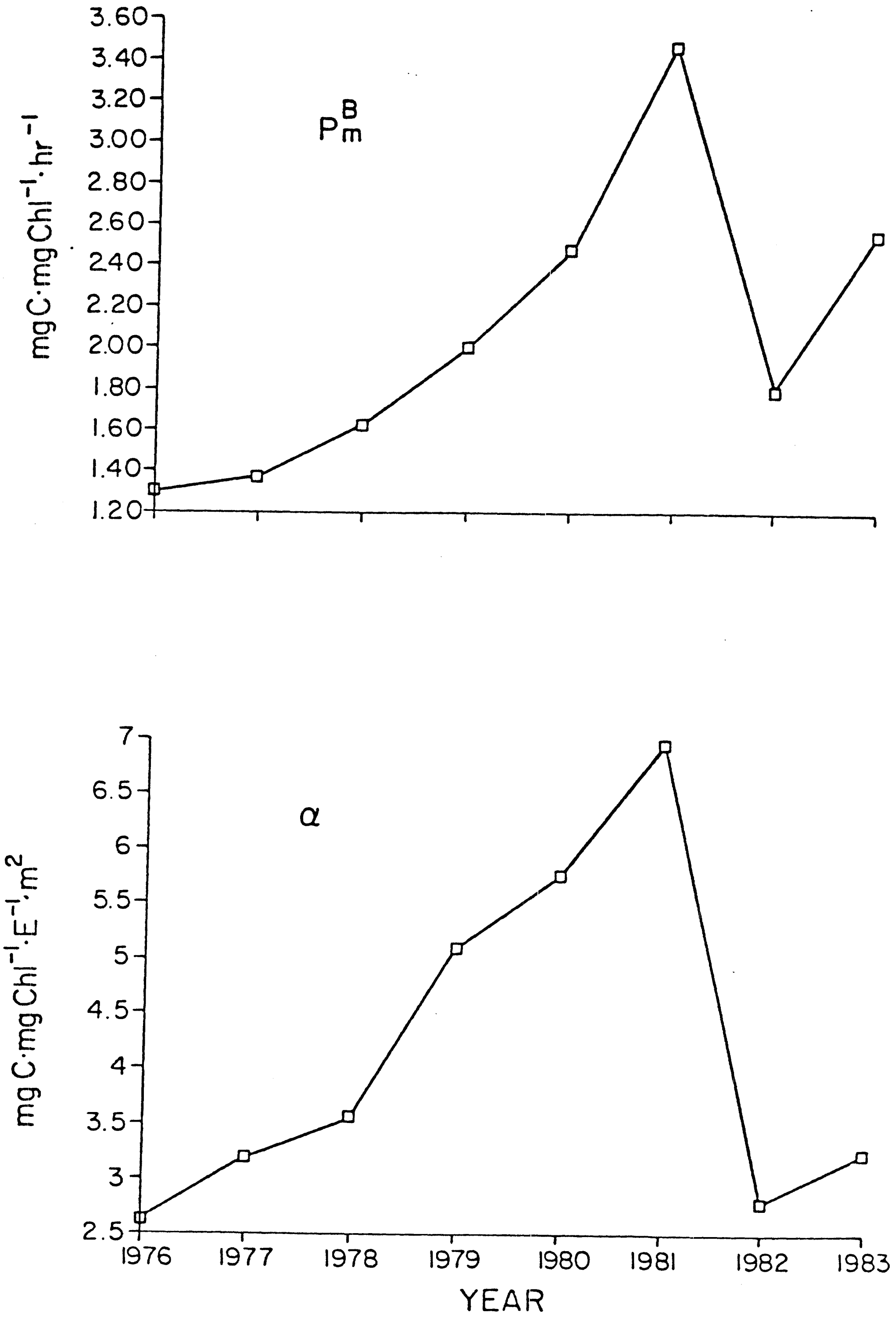

FIG. 4. The annual means of photosynthesis parameters in lakes of the Experimental Lakes Area, northwestern Ontario. See Fee et al. (1987) for details.

Great lakes are also good sites for studying how ecosystems of different ages respond to perturbations. For example, Lake Michigan is being cited as a classic example of how "trophic cascades" (Carpenter et al. 1985) work. According to this hypothesis, introductions of exotic fish species into Lake Michigan (age ~10,000 years, total number of fish species 100) have had a "cascade" of trophic effects: changes in zooplankton composition which resulted in changes in the phytoplankton species composition and thus changes in water quality parameters such as transparency. However, extrapolation of theories such as this - developed in the very young Great Lakes - to much older great lakes is obviously unwarranted. This is not a moot point, as the introduction of an important pelagic planktivorous fish from nearby ancient Lake Tanganyika (age ~10,000,000 years, total number of fish species ~400; basin ages from Hecky 1984) - which has more species of fish than any other lake in the world - has been seriously proposed. The "trophic cascade" hypothesis would predict that such an introduction would almost certainly have dire consequences such as altered ecosystem structure (increased algal crops) and species extinctions. But the role of species diversity in buffering biological perturbations is unknown; indeed, the general influence of species diversity in lakes is unclear. Species rich lakes like Lake Malawi may be less prone to wild biological changes following the introduction or removal of any individual species than lakes like Great Bear Lake or Lake Michigan. If this were true, then the introduction could provide a high yield of fish which would be of great benefit to the protein starved countries surrounding Lake Malawi. Alternatively, the possibility of massive extinctions has been argued because of the overspecialization of this isolated and highly evolved fish community. In any case, the point that we are making is that the ability to examine actual functioning ecosystems with such a wide range of ages cannot be as easily done anywhere else on the earth, and especially not in the ocean, which is a single interconnected system with a very great age.

Another time scale that great lakes can help illuminate is that of the residence times of chemical species, particularly those that limit phytoplankton growth (phosphorus, nitrogen, and silica). For example, the residence time of phosphorus varies from a few years in Lake Erie to millenia in Lake Tanganyika. Do long residence times for nutrients stabilize biological production processes proportionately? Such questions cannot be studied in the ocean because it has only one residence time for any element (much longer than in lakes).

TOOLS FOR GLOBAL STUDIES

The time is right for launching systematic investigations of global phenomena because powerful tools - especially satellite remote sensing and inexpensive data processing equipment - have only recently been generally available. Satellites allow us to determine the spatial distribution of variables like chlorophyll, transparency, turbidity, and temperature in an entire great lake at an instant in time. These instruments operate across jurisdictional boundaries and in all parts of the globe, thus greatly simplifying data collection from remote great lakes in a standardized, repetitive manner.

Being able to remotely sense an entire great lake at once is a great advantage that can't be duplicated in ocean studies, where repeated satellite passes yield views of systems that are variably influenced by mixing and advection across open boundaries. At the other end of the size spectrum, great lakes are more appropriate subjects for remote sensing than small lakes because their deeper mixed depths and the weaker development of metalimnetic and hypolimnetic algal blooms in them mean that a greater percentage of their total biological activity occurs in their upper mixed zones, which are accessible to remote sensing instruments. Further, if our "central hypothesis" is true, then there will be less uncertainty in productivity estimates derived from remotely sensed chlorophyll data in large lakes than in small ones. However, these are clearly only broad generalities and a great deal of research needs to be done before we will be in a position to predict the suitability of the different remote sensing techniques for water bodies of different sizes.

Just as important as the spatial information that they provide, satellites allow us to follow variables over time scales of years to decades with a standardized methodology. A major use of remote sensing will, therefore, be monitoring aquatic systems over time. This will allow us to detect water quality changes without having to support expensive on-lake monitoring programs for individual great lakes (see e.g., Hecky and McCullough 1984).

We are just beginning to appreciate how remote sensing will change the nature of great lakes research in the decades to come. Biologists will develop productivity models driven by remotely sensed chlorophyll and transparency data. From these results, trophic-dynamic theory can be used to set maximum sustainable fishery yields. Physicists will develop data sets on circulation patterns on the order of years. Geologists will be able to determine long-term weathering patterns in entire drainage basins.

Of course, every methodology has its limitation, and we need to define what the limitations of remotely sensed data are. Probably the most serious general limitation is that these instruments can only give information about surface characteristics of great lakes. We thus need work on determining how surface properties relate to what is happening within great lakes. This will involve shipborne advanced acoustic methods as well as aircraft deployed expendable profilers that look "inside" great lakes, to flesh-out the two dimensional picture given by satellite imagery. Data on heat content, heat fluxes, currents, surface and internal waves, as well as populations of fish and invertebrate animals on spatial scales up to whole lakes will be forthcoming from these instruments. By linking in situ instruments with satellites for data transmission, great lakes limnologists will be able to measure three-dimensional properties of these lakes on increasingly long time scales.

Another major area of work will be determining confidence intervals for remotely sensed data. This is a major undertaking that will require close collaboration between the agencies responsible for gathering satellite imagery and limnologists that have the expertise for obtaining in situ great lakes data. Such work is currently hindered by high costs as well as

by the long lags between the time that satellite images are obtained and when they are available to the research community. There will be great advances in the technology associated with this area in the next decade. For example, the information that previously required a dozen magnetic tapes and a mainframe computer to analyze can now be put on a single compact disk that can be analyzed on a personal computer. The next generation of personal computers will have processing capabilities comparable to the current mainframes. Hopefully, information processing techniques will both increase in sophistication and drop in price to the point where real-time satellite imagery can be routinely used to locate research vessels for sampling purposes.

Remotely sensed biological variables are probably the hardest to calibrate. Even if we assume that the enormous technical problems of remotely sensing chlorophyll in fresh waters will be overcome, we are going to have difficulty interpreting these data because we know so little about the spatial and temporal variability of the ratio between chlorophyll concentration and phytoplankton production. The literature now contains values for the critical transfer parameters α and Pm^B that span more than two orders of magnitude. It is unclear how much of this variation is real and how much is an artifact of the multiplicity of methods that have been used to measure both primary production and chlorophyll concentration. Until we can predict the values of these parameters as functions of "mappable" variables such as lake size, position in hydrologic network, latitude, and geological setting, each satellite image will need surface calibration.

CONCLUSION

To date, great lakes research has contributed surprisingly little to our understanding of phenomena that operate on long space and time scales. This has resulted from the fact that past efforts have been almost entirely short-term (a few weeks to a few years), site-specific, and have been done almost exclusively on the Laurentian Great Lakes. In order to realize the potential of great lakes for studying global phenomena, we must adopt new research perspectives. In particular, great lakes located in tropical and subarctic environments deserve much more attention than they have been given: these lakes provide us with extremes of temperature, mixing depth, age, and geological history which will allow us to develop and test global hypotheses.

Another problem that has retarded work on global space and time scales is that existing great lakes data have been gathered with a confusing variety of methods. For example, there has been extensive work on phytoplankton primary production in all of the Laurentian Great Lakes but virtually none of these data are directly comparable. Thus, basic questions such as "Is the ratio between chlorophyll concentration and primary production constant enough that we can use remotely sensed chlorophyll measurements to map productivity in the Great Lakes?" cannot now be answered even though data apparently relevant to this question have been gathered for over 30 years. Limnologists must adopt standard methods in order to obtain results that can be compared from lake to lake or over long time periods.

The other great need is to consciously consider larger spatial and temporal scales when planning research programs. We have a great deal of information about phenomena that operate over time scales of days to years and spatial scales of 1 to 100 kilometers, but we know virtually nothing about processes that operate on time scales of several years to decades or spatial scales of whole great lakes. Yet it is through these longer time and space scales that large water masses interact with the atmosphere and the land. There is a great need for expanding great lakes studies to include these currently neglected time and space scales. Without information on natural (background) variability of great lakes on these longer time and space scales we will continue to have difficulty separating local noise from global signal in our data.

Resolution of large space- and long time-scales requires greater cooperation among biologists, physicists, and geologists, the collection of long time series, and a change in the emphasis of funding organizations away from short-term projects with quick payoffs to much longer-term global scale observations. This will require much tighter program integration with careful attention to the problems of archiving biological and chemical samples, and avoidance of confusing methods changes and personnel changes. Finally, support for these programs needs to be on the scale of decades; otherwise, there is a great risk of incomplete work.

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APPENDIX B2

BIOGEOCHEMICAL PROCESSES AND CHEMICAL FLUXES

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A vast number of processes and variables govern the transport, reactivity, and fate of elements within an ecosystem as large as the Great Lakes (Fig. 1). Because elements circulate among the numerous and varied geologic and biologic compartments within the ecosystem, we have termed the study of these cycles "biogeochemistry" (Likens et al. 1977). Understanding the pathways along which elements move and the rate with which they travel is fundamental to understanding how the Great Lakes operate as unique ecosystems, how the diverse biologic components within them live and die, and how the systems change or maintain themselves through time.

Taken as a whole, the ecosystem may be visualized as a matrix of chemical pools, some living, some nonliving, interacting on time scales from seconds to centuries and on space scales from microns to thousands of kilometers. The processes under study and tools used to study them, therefore, range from remotely sensed global and regional changes to molecular scale interactions at reactive interfaces. A major goal of biogeochemistry is to place these individual interacting compartments within the framework of the whole system and within the context of regional or whole lake dynamics. These dynamics, e.g., long-term climatic variations, seasonal patterns, large scale water movements, aperiodic storm events, or pulse invasions of key alien organisms (see e.g., Scavia et al. 1986) are uniquely "ecosystem processes" because of the time and space scales over which they operate. The future impact of either controllable or uncontrollable variables will not be adequately predicted until we understand the regional and whole lake cycles of the biologically important elements in the Great Lakes and the dynamic processes which control them.

The purpose of this overview is not to review all that is known about the biogeochemical cycles in the Great Lakes but to serve as a departure point from which we may discuss the gaps in our knowledge and, hopefully, the direction of future studies.

THE GREAT LAKES: UNIQUE AQUATIC SYSTEMS

Without question the Laurentian Great Lakes are unique. Because of their size they are different than all other freshwater ecosystems in the world. They are large, they are deep (>400 m), they are young (~a few thousand years), and they are impacted by industrialized society. They are also, for the most part, closed systems -- an attribute of decided advantage to the biogeochemist. Because they are large, they are truly plank-

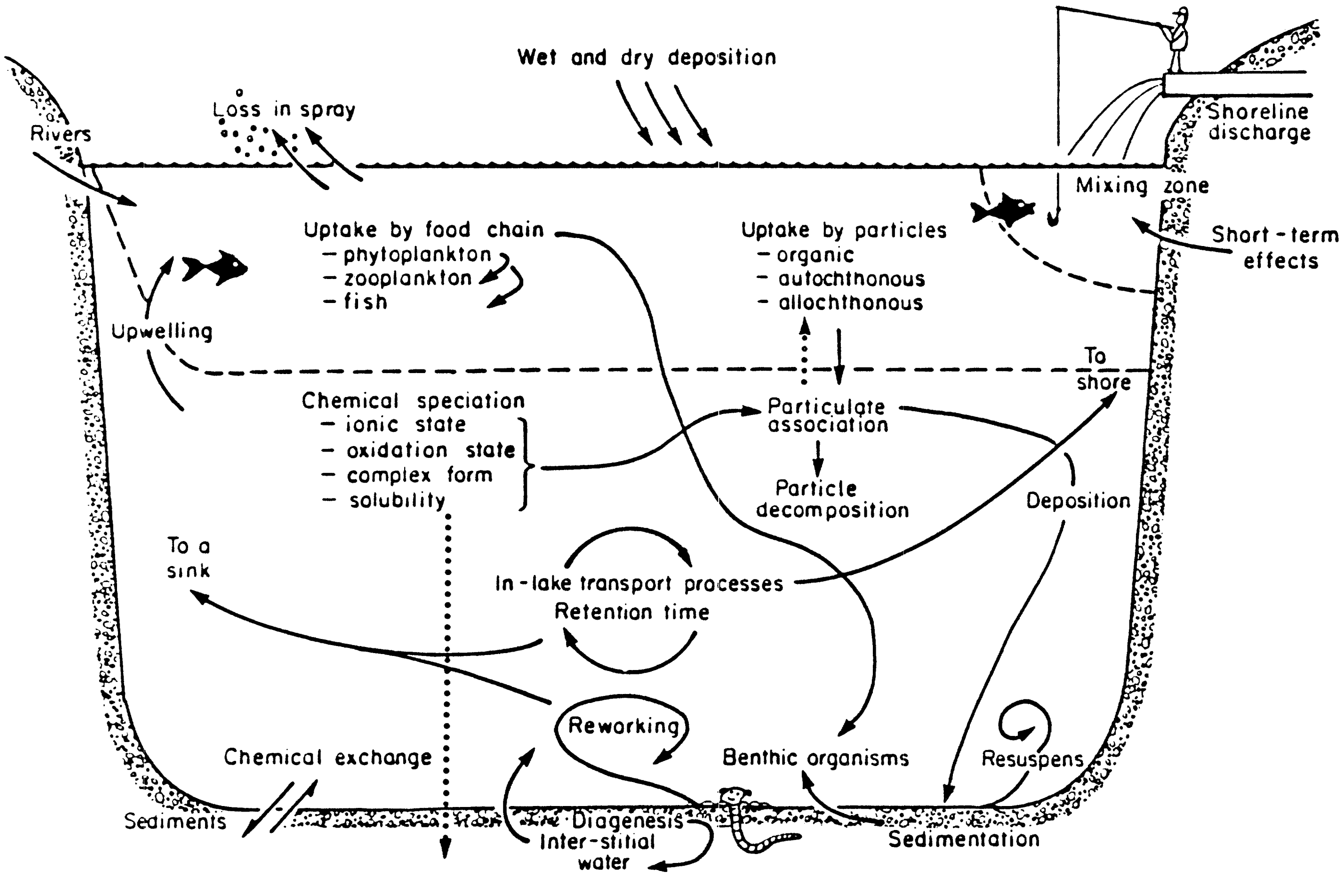

FIG. 1. Biogeochemical pathways in the Great Lakes.

tonically dominated ecosystems (as opposed to littoral dominated systems as in the case of their smaller cousins). Because they are mostly deep, yet not too deep, they contain a significant benthic/detrital food chain fed largely by pelagic production. Because they are young, they are evolutionarily "uncomplicated," i.e., much less diverse biologically than their saltier big sisters -- the world's oceans. And, finally, because their shores are populated by several millions, they have been irreversibly altered in fundamental ways.

BIOGEOCHEMISTRY: THE IMPORTANCE OF SCALES IN TIME AND SPACE

In the detailed study of the biogeochemistry of an ecosystem we are generally forced to divide the system into individual compartments through which chemicals flow. At its simplest level this may be represented by a series of interconnected elemental pools linked via chemical fluxes which transform elements from one pool to the next. Ideally we would like to be able to quantify both the size of the pool and the fluxes into and out of the compartment in question.

A very useful concept, the resident time, TR, of an element in any reservoir or pool is frequently calculated as:

$$TR = \frac{A}{dA/dt}$$

where A = the total amount of the element in the pool (also frequently referred to as the total inventory or standing stock), and dA/dt = the addition or removal rate. In a recent review, Wangersky (1986) discussed the usefulness of this concept and the requisite assumptions behind it. The principal implicit assumption is, of course, that the reservoir is in a steady state, or, simply put, is not changing in size through time.

It is more frequently the case that biogeochemists cannot quantify all the transport rates or fluxes to and from each chemical reservoir. Hence mass balances, in which outputs are matched against inputs, are often difficult to achieve. In order to understand the dynamics of the reservoir, e.g., how quickly it turns over (i.e., its residence time), therefore, requires a measure of the pool size and the time or space scales over which it is in steady state. Obviously if the pool is increasing or decreasing in size then residence times calculated from fluxes may be seriously in error. The biogeochemist, therefore, must generally assume a steady state in time and space which matches the scale of the process under study.

In general, the more geologic the process the longer the time scale, and the more biologically mediated the process the shorter the time scale. Likewise as space scales decrease time scales tend to increase. In the Great Lakes residence time calculations for many elements are simplified by the fact that the upper Great Lakes (Superior, Michigan, Huron) are essentially closed systems and losses due to outflow are frequently insignificant or easily quantified. The water retention times (volume/outflow) for these three lakes are 190, 100, and 30 years, respectively (Wahlgren et al.

1980). Even in the lower Great Lakes inflows and outflows are well known and mass balance budgets are possible. Because of their size the Great Lakes encompass a greater range of time and space scales than all other freshwater ecosystems. Knowing the distance in time and space over which a biogeochemical process operates determines both the analytical approach (e.g., how big a sample and how often collected) and the application of the useful steady state assumption. Two brief examples, provided by colleagues, illustrate the point.

1. Boraas's Bottle. A colleague suggests that the middle of Lake Michigan is the closest thing we have to a "bottle without walls." Because of the size of the lake, the nearshore is sufficiently remote so that during certain times of the year it has a minimal influence on the mid-lake planktonic community. Under these conditions the lake serves as a sort of large culture experiment, in which natural biological and chemical interactions may be studied without laboratory induced artifacts. Questions which naturally arise include: how big is this bottle, and over what time scales is it at steady state? The size of the system gives us the unique potential of studying mesoscale phenomena over distances of meters to kilometers and over periods of weeks to months. Such processes cannot be studied in the laboratory.
2. Nealson's Nodules. The importance of how we frame our assumptions of steady state is illustrated by another colleague studying manganese nodules. Radiometric measurements indicate that the growth rate of some freshwater manganese nodules is on the order of a few mm per thousand years. At this growth rate, however, the size of these nodules would indicate they are older than the lake in which they occur. Clearly, some assumption is wrong. Biogeochemically, the system apparently is not at steady state over a geologic time scale, although it may be at steady state over much shorter time scales. The mass balance of today may not be applicable to the mass balance of several thousand years ago.

BIOGEOCHEMICAL PROCESSES

The fate of elements within the ecosystem is frequently controlled by the processes through which elements are transferred from one compartment to another. Exchanges across these boundaries or interfaces are often the rate determining steps in biogeochemical cycles. Changes in oxidation state, chemical form, mobility, etc. are determined by the diffusion, advection, and reaction occurring at the interfaces between one chemical pool and another. The point of actual kinetic control may be the cell wall of an organism, a diffusive boundary layer, or any one of a variety of other interfaces. Over the last decade or so, biogeochemical studies in the Great Lakes have tended to focus on several major boundary or interface processes. These include:

1. Air-sea exchanges
2. Particle-water or particle-solute interactions
3. Sediment-water exchanges
4. Aquifer-lake exchanges
5. Land-water coupling

The following discussion will briefly consider all but the last of these, which is considered elsewhere. This is, by and large, an organizational choice around which to orient the discussion, but also reflects the emphasis of the research which has been done to date.

ATMOSPHERE-LAKE INTERACTIONS

The atmosphere is a source for a variety of elements, gases, and trace organics. The interaction between the troposphere and the Great Lakes occurs for the most part on a regional scale, as indicated by isopleths of acid rain, atmospheric ammonia, etc. (Fig. 2; Junge 1958). Whereas carbon dioxide is distributed globally, the oxides of nitrogen and sulfur, particulate phosphorus, and trace organics tend to fall out near their sources (i.e., within $<10^6$ m) (Reiners 1983). Atmospheric transport processes vary in scale from very local to global and can rapidly transport airborne constituents from remote sources to the Great Lakes, as evidenced, for example, by the ^{131}I (half life ~8 days) detected in rainfall over Lake Michigan within a few days of the Chernobyl accident (D. N. Edgington et al., unpublished data). Gas exchange with the atmosphere is controlled by both mixing processes in the lake and exchange mechanisms at the air-water interface. Complete ventilation of the lakes occurs at overturn, and after stratification hypolimnetic water is, for the most part, isolated from atmospheric contact as shown by the ^3He-tritium water mass ages of Torgersen et al. (1977) (Fig. 3).

Exchange processes across surface films at the air-water interface have been discussed by Liss (1975), Duce (1983), Eisenreich (1982) and others (see Fig. 4). Atmospheric deposition is a significant source for some trace metals, e.g., Pb, Zn, Cd, Cu (Elzerman and Armstrong 1979, Armstrong and Elzerman 1982), and for certain atmospherically borne trace organics, notably chlorinated hydrocarbons and polynuclear aromatic hydrocarbons (Andren 1983, Eisenreich et al. 1981). In the 100 micron thick layer containing even thinner surface films, these constituents, as well as naturally occurring hydrophobic organic materials (Meyer and Kawka 1981), may be enriched several fold above concentrations in bulk lake water. Surface films may also be slightly enriched in total numbers of bacteria by 10 to 20 fold (Crawford et al. 1982). Residence times for Fe, Al, Mn, Pb, Cr, Zn, and Cd in Lake Superior surface films have been estimated to be 16 to 83 minutes, sufficiently long for chemical/physical/biological reactions to occur (Eisenreich 1982).

Because of the large size of the surface area of the lakes relative to their drainage basin, atmospheric inputs can be significant. Atmospheric fluxes to the Great Lakes have, therefore, received considerable attention and are reasonably well known for a variety of elements (e.g., P, organic C, SiO_2, SO_4, NO_3, chloride, Ca, Mg, Na, K, Fe, Al, Mn, Cu, Cd, Pb, Zn, Ni, PCBs) (e.g., Eisenreich et al. 1977). Volatilization losses, i.e., the flux from the lake to the atmosphere, for some exotic organic contaminants have also been estimated with some accuracy and are equivalent to losses to the sediment (Swackhamer and Armstrong 1986). Chemical and biological reactions at the air-water interface are less well known, occur rapidly, and therefore are difficult to assess quantitatively. Photooxidation, reaction with OH radicals, and biodegradation by bacterioneuston are examples.

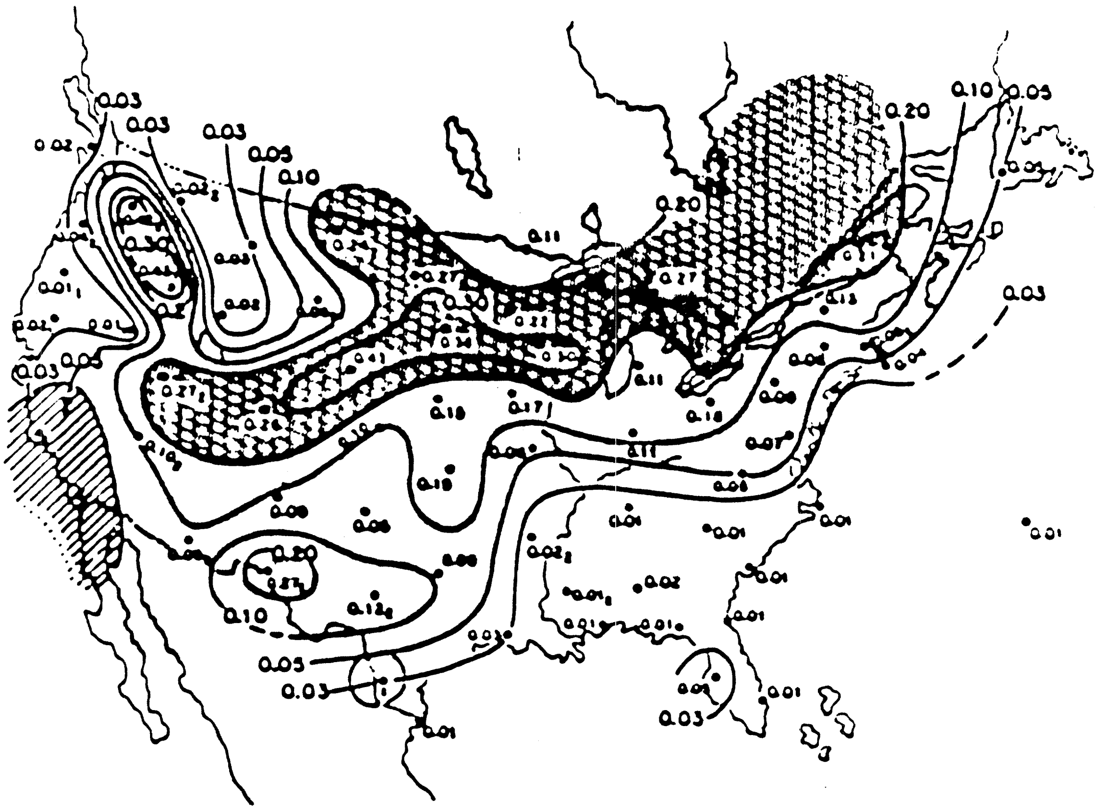

FIG. 2. The distribution of atmospheric components, here ammonia, indicates the space scales over which the atmosphere interacts with the Great Lakes (from Junge 1958).

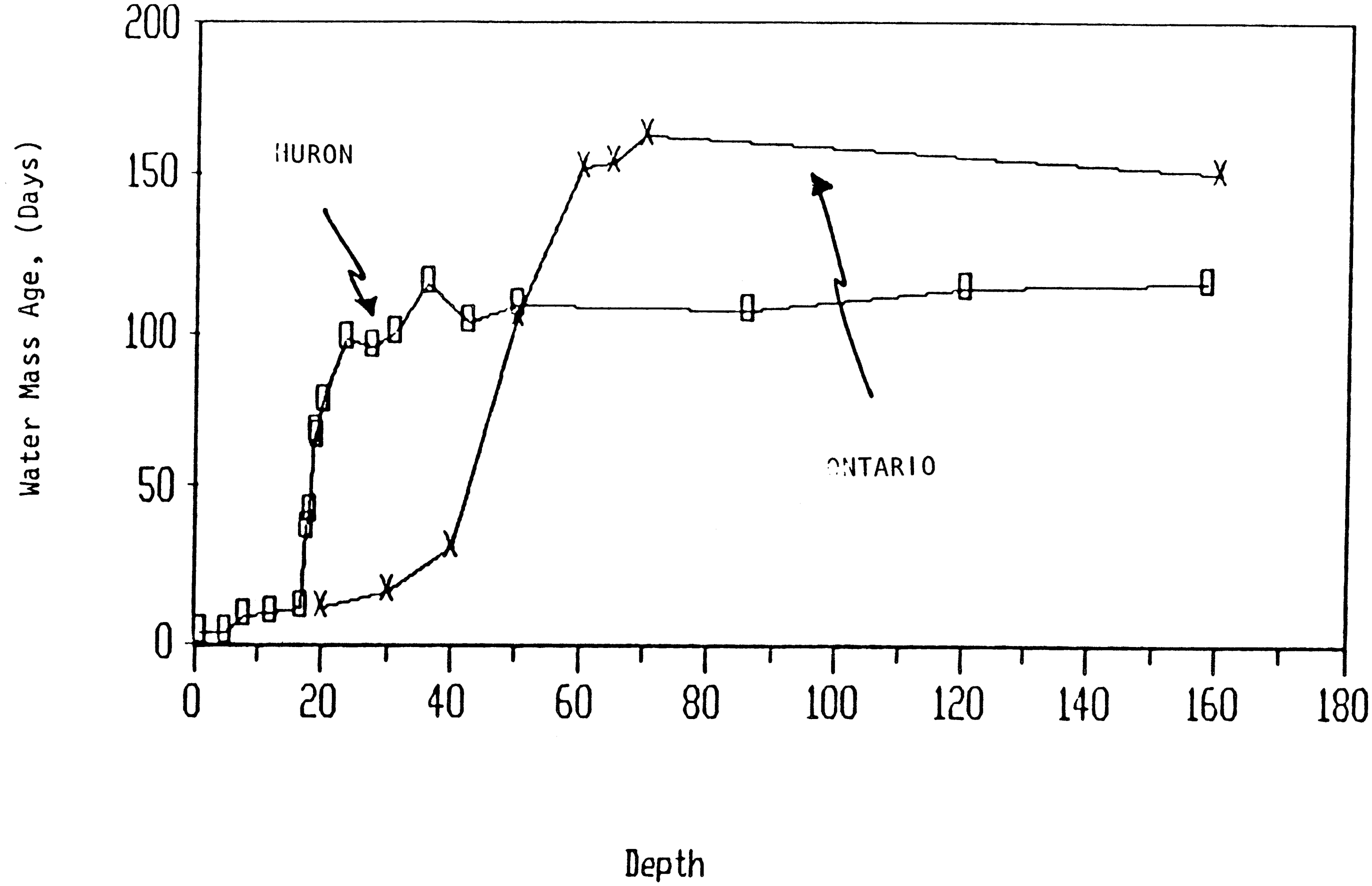

FIG. 3. Helium-3/tritium water mass ages for profiles in Lake Huron and Lake Ontario (from Torgersen et al. 1977). ▭ = Lake Huron, X = Lake Ontario.

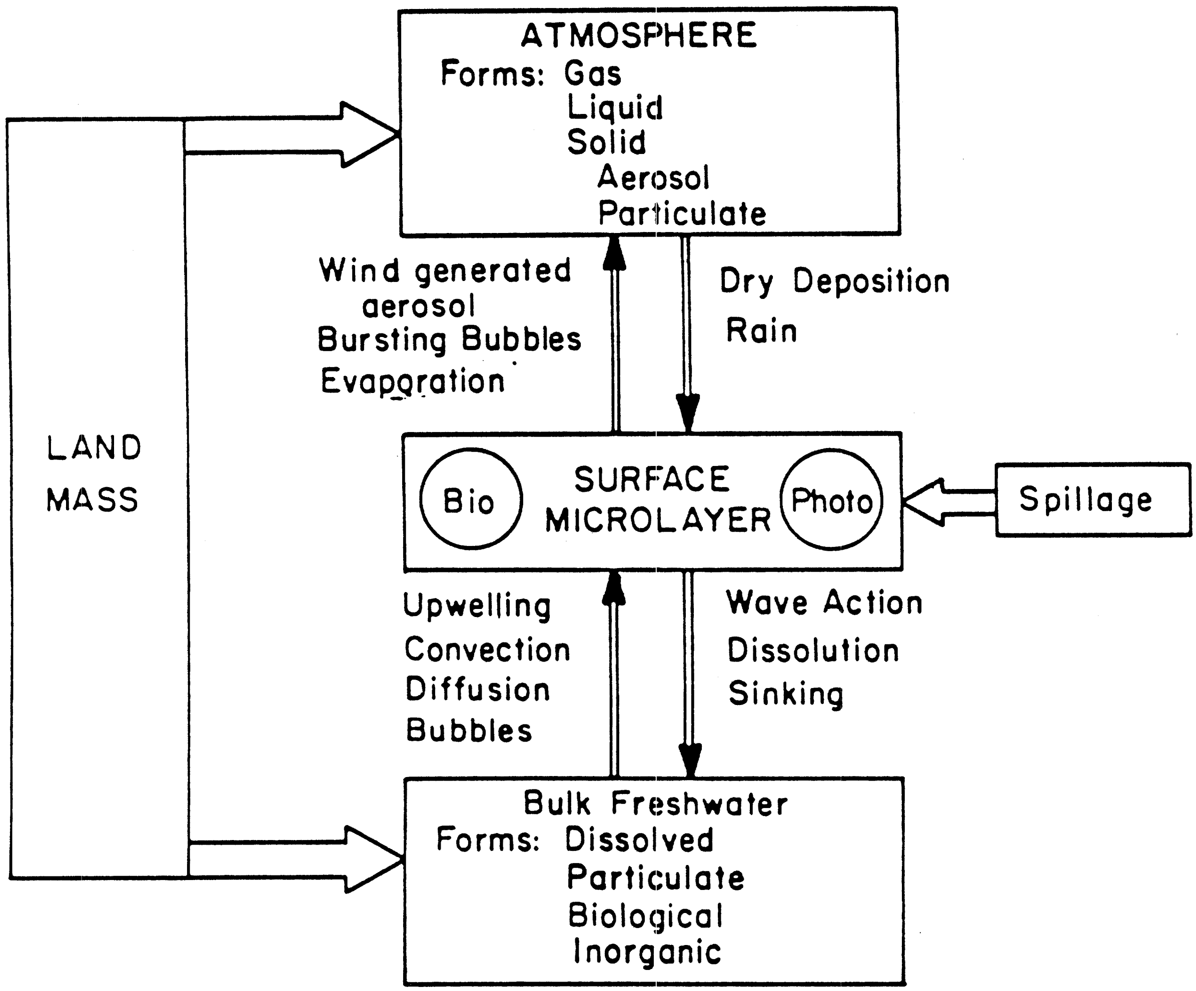

FIG. 4. Sources and sinks of major and trace metals for freshwater surface films (from Liss 1975 by way of Eisenreich 1982).

PARTICLE-SOLUTE INTERACTIONS

Types of Interactions

The chemistry of particle-solute interactions in aquatic environments is both complex and important and has received considerable attention from both a theoretical and empirical standpoint (Stumm and Morgan 1981). Transport pathways are often controlled by the specific type of element-particle selectivity which may enrich elements and chemical compounds in certain phases or types of particulate matter. Biogeochemical cycles for many elements and inorganic and organic compounds are determined by the processes affecting particle production (e.g., primary production, $CaCO_3$ precipitation) and particle removal (e.g., sedimentation and dissolution). Important types of particle associations in the Great Lakes include (from Armstrong and Andren 1986):

a) Biological assimilation -- nutrient uptake is the most obvious example
b) Affinity for organic surface coating on particles
c) Adsorption by hydrous metal oxide surface coatings
d) Coprecipitation with a calcium-carbonate matrix
e) Surface adsorption by calcium carbonate particles or coatings.

For the elements of major biogeochemical importance, i.e., carbon, nitrogen, phosphorus, sulfur, and other micronutrients, the first type of "particle association" is far and away the most important. The details of nutrient uptake are complex, however, and are controlled by biotic interactions among phytoplankton, zooplankton, and bacteria. Our understanding of these food webs, "microbial loops," etc., has expanded greatly of late but is still something of a mystery and an active area of current research. Knowing the fate of carbon, nitrogen, phosphorus, and sulfur in the environment tells us a great deal about the fate of a host of other elements as well.

The Role of Particle Production and Removal: Examples Using Trace Constituents

The distribution and abundance of suspended particles varies on a seasonal basis (Table 1). The residence times for elements in the water column will vary significantly depending upon the controlling particle association and particle production and removal rates. For example, the input and removal of Pb-210 from the waters of Lake Michigan can be modelled as a steady state process on an annual basis (Van Hoof 1985). However, over shorter time scales non-steady-state processes control the removal of Pb-210 (and, by analogy, other elements as well) as indicated by Pb-210 water column residence times. Van Hoof (1985) reported variations in these residence times from days to months depending upon particle production and removal processes (Table 2). Two episodic particle production events are important to annual Pb-210 removal rates:

1) the spring diatom bloom and subsequent fecal pellet production and fallout which contributes an estimated 20-25% of the apparent total Pb-210 flux

2) the precipitation of $CaCO_3$ which was estimated to transport 20-30% of the annual Pb-210 input to the lake.

TABLE 1. Seasonal particle events in Lake Michigan (after Shafer and Armstrong, in prep.).

Period:	Fall overturn to spring diatom	Spring diatom bloom	Stratified period	Stratified period whiting event
Conditions:	Isothermal	Largest input of particle	Epilimnion uncoupled and sparsely populated	$CaCO_3$ in epilimnion reaches 1,600 $\mu g \cdot L^{-1}$
	Vertical particle profiles (400-500 $\mu g \cdot L^{-1}$)	Vertical particle profiles (1,100 $\mu g \cdot L^{-1}$)	Subthermocline chlorophyll maxima	
	Particle types mostly detrital resuspended sediments	Diatoms		$CaCO_3$ settles out with most reaching bottom before dissolving

TABLE 2. Residence times for Pb-210 in Lake Michigan (Van Hoof 1985).

Pool	Season	Residence Time
1) Total (dissolved and particulate) epilimnetic Pb-210	Whiting period $CaCO_3$ ppt.	< week
	Fall	~few months
2) Particulate PB-210 whole water column	Whiting period	20-30 days
	Non-whiting, stratified (summer)	50-100 days
3) Dissolved Pb-210 whole water column	Winter-early Spring	2-3 months
	Summer	2.5-5 months
	Fall	4-9 months

These two events also appear to control the seasonal cycle of plutonium in the epilimnion (Wahlgren et al. 1980). It has been pointed out (Sholkovitz and Copeland 1982), and is worth reiterating, that despite the fact that these non-steady-state events result in a transient complexity not present in the oceans, natural time dependent variations can be very useful in establishing the dynamics of biogeochemical cycles. In that regard the Great Lakes are sometimes nicely placed between the oceans steady state and the idiosyncracies of smaller lakes.

RESUSPENSION

Dominant features of the biogeochemical cycles of particle associated constituents in the Great Lakes are the processes of sedimentation and resuspension. Sediment traps deployed at intervals of a few meters above the lake bottom consistently show exponentially increasing particle collection rates (g cm^{-2} d^{-1}) as the sediment-water interface is approached (Wahlgren et al. 1980, Eadie et al. 1984). Most resuspension appears to be confined to the upper 10 - 15 meters of the water column above the lake bottom (Fig. 5). Particles collected in these near-bottom traps are more similar in their chemical composition to bottom sediments than to material collected in near-surface traps.

The mechanisms and dynamics of benthic nepheloid or other boundary layers have received some attention in the Great Lakes (e.g., Marmorino et al. 1980, Chase and Tisue 1977) but remain largely unknown. Recently Mortimer (1987), using satellite images of Lake Michigan, has pointed out correlations between coastal currents, thermal bar formation, and resuspensions in the nearshore zone (<20 km).

The role of resuspension/sediment mixing and the distribution of a chemical pollutant between particles and water has been modelled for the Great Lakes based upon (Edgington and Robbins 1976):

1) distribution coefficients for the constituents of interest (termed KD = mol g^{-1}/mol mL^{-1}), and
2) the time to ultimate particle burial in sediments below the reach of mixing by organisms or physical resuspension.

For constituents with KD >10^3 to 10^4, particle-water interactions and resuspension combine to reduce the concentration of a pulse input of a pollutant in solution initially, but to prolong its presence in solution in time. Because sediment resuspension/mixing processes expose sediments equivalent to several decades of sediment deposition, the sediments act as a "capacitor" in the system, integrating inputs over a period of years.

The role of sediment resuspension in nutrient cycling is not entirely clear. What is known is that the majority of the primary production occurring in Lake Michigan, for example, is supported by regenerated nutrients. "New" nutrient inputs are estimated to be only 5 to 10% of the total required to support primary production. In the case of silica, perhaps <5% of the annual Lake Michigan silica requirement enters via watershed inputs (Parker et al. 1977) and the remainder results from the dissolution of diatom frustules within the hypolimnion and surface sediments of the lake

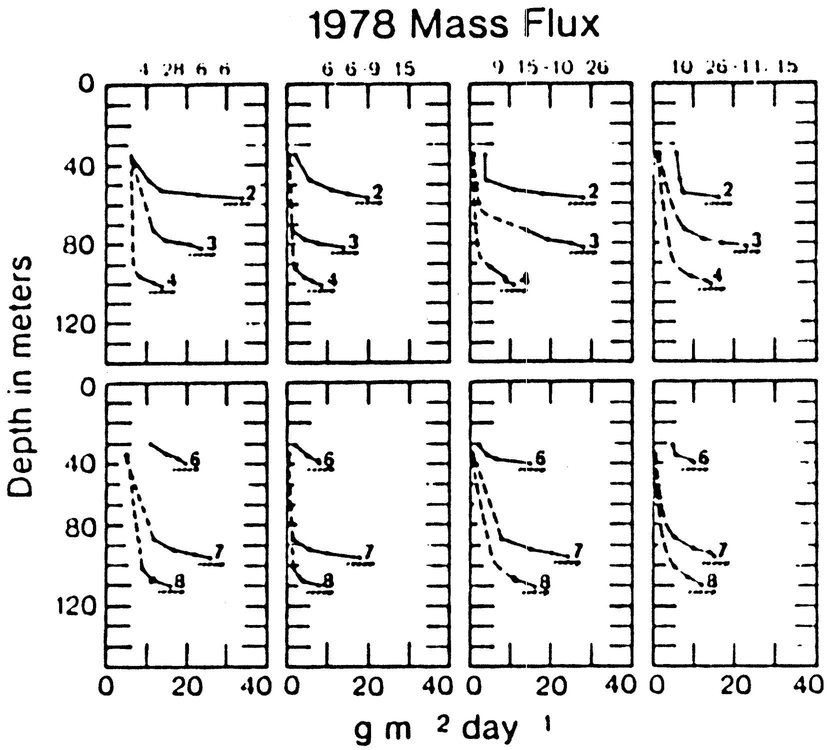

FIG. 5. Mass flux profiles for sediment trap data on Lake Michigan. Units are $g/m^2/d$. The four panels correspond to four collection periods. The numbers correspond to station locations with numbers 1 and 5 being ~ 3-4 km offshore of the Grand River, 2 and 6 being ~ 8-10 km offshore, and 3 and 7 ~ 15 km offshore (from Eadie et al. 1984).

(Conway et al. 1977). Budget calculations for the regeneration of silica in Lakes Ontario, Erie, and Superior yield similar conclusions (Nriagu 1978, Johnson and Eisenreich 1979). Resuspension may play a role in this recycling. Since phosphorus recycles at a faster rate than silica, a greater percentage of the total P regeneration would seem to occur in the epilimnion, with silica regeneration occurring to a greater extent in the hypolimnion. One might speculate that this segregation in rates and sites of recycling would logically result in an increase in the P:Si ratio as surface water with a greater relative phosphorus content maintained by rapid regeneration moves downstream [this is analogous to the same processes resulting in the higher relative silica content of the deep North Pacific vs. the deep North Atlantic (see Broecker 1974)]. If 95% of the silica required by diatoms annually is regenerated, then the residence time for silica in the lake will approach 20 years. Over this time scale, even with long water retention times, outflow losses, as well as losses to the sediment (i.e., burial) need to be considered (Schelske et al. 1986).

Based upon 4 years of sediment trap data, Eadie et al. (1984) have constructed organic carbon and phosphorus budgets for a 100-m-deep water column in Lake Michigan. The principal features of the organic carbon mass balance (shown in Fig. 6) are that only ~20% of the primary production estimated by Fee (1973) crosses the thermocline, and only one-third of this apparently reaches the sediments to be permanently buried. Regeneration and remineralization processes account for ~94% of the carbon fixed within the photic zone. These calculations are, of course, heavily dependent upon primary production estimates. Assuming a Redfield C:P ratio (106:1) results in a similar mass balance for phosphorus which is not changed dramatically by higher stoichiometries (Gachter and Bloesch 1985) (Fig. 7).

SEDIMENT ACCUMULATION AND REDISTRIBUTION

Resuspension into the benthic nepheloid layer calculated from sediment traps is equivalent to roughly 10 times the local sediment accumulation rate for both carbon and phosphorus. Wahlgren et al. (1980) pointed out that it is impossible to balance the downward flux of plutonium measured in sediment traps with that apparently deposited annually in the sediments at the same location because of subsequent horizontal redistribution within the lake of older sediments containing plutonium.

Comparing changes in the Cs-137 distributions in the sediments of the southern basin of Lake Michigan from 1972 to 1982, Benante (1984) has shown that such sediment "refocusing" is significant. Figures 8 and 9 give the sedimentation rate distributions for 1972 (Edgington and Robbins 1976) with those calculated from recoring the same stations 10 years later. Figure 10 shows the relative change in the Cs-137 inventories over this 10-year period. 93% of the total Cs-137 measured in 1972 was recovered in 1982. Areas with a 1982 to 1972 ratio of total Cs-137 less than 1.0 represent zones where horizontal sediment migration has resulted in a loss of Cs-137; areas with a ratio greater than 1.0 represent zones where migration has resulted in a gain.

It is interesting to note that sediment accumulation does not follow bathymetry as in the case of most small lakes, but is focused on the eastern slope, presumably as a result of the predominant counterclockwise cir-

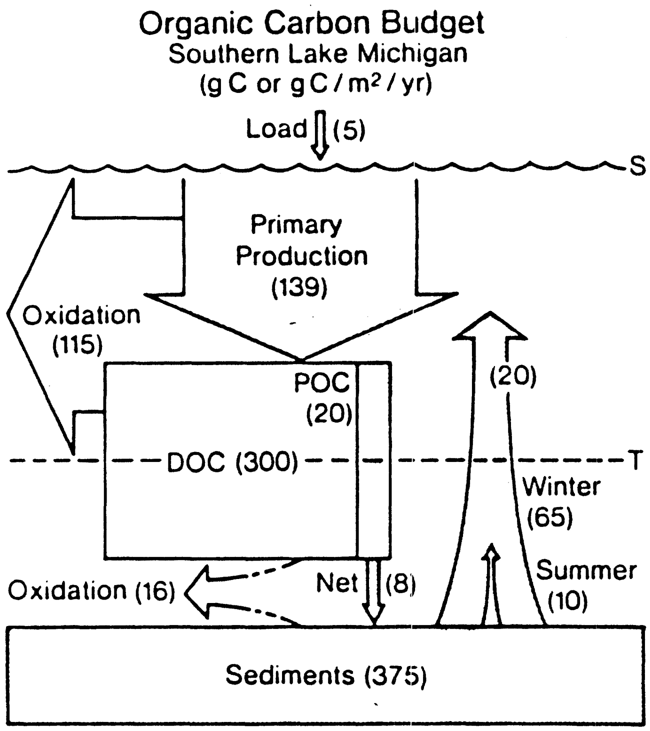

FIG. 6. Organic carbon budget for a 100-m-deep, 1 m^2 water column in southern Lake Michigan. Shaded areas represent particulate organic carbon. Numbers in boxes (reservoirs) have units of g C. Numbers associated with arrows (fluxes) have units of g $C/m^2/yr$. Widths of arrows and boxes are proportional. T (dashed line) represents the thermocline (from Eadie et al. 1984).

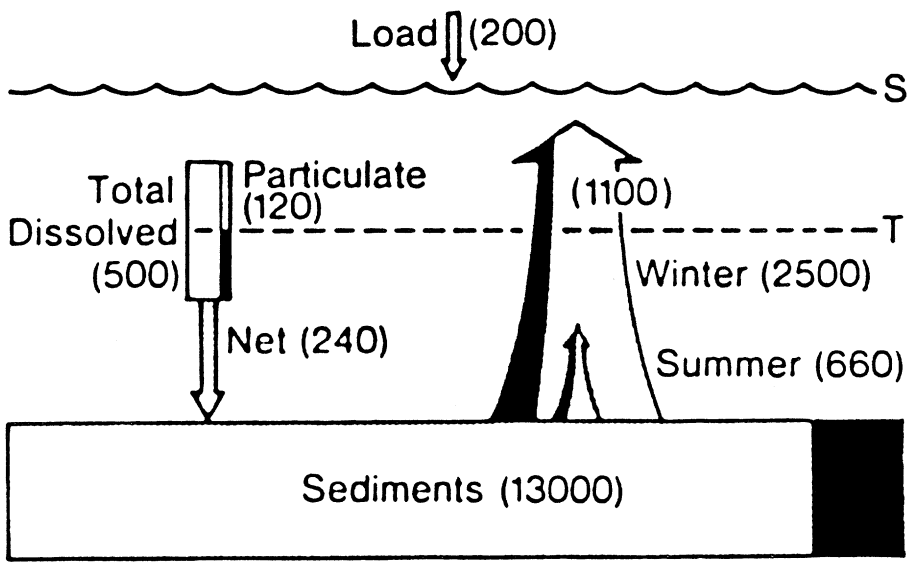

FIG. 7. Phosphorus budget for a 100-m-deep, 1 m^2 water column in southern Lake Michigan. Shaded areas represent particle-bound phosphorus. Black areas represent 0.1 N NaOH extractable P. Numbers in boxes (reservoirs) have units of mg P. Numbers associated with arrows (fluxes) have units of mg $P/m^2/yr$. Widths of arrows and boxes are proportional. T (dashed line) represents the thermocline (from Eadie et al. 1984).

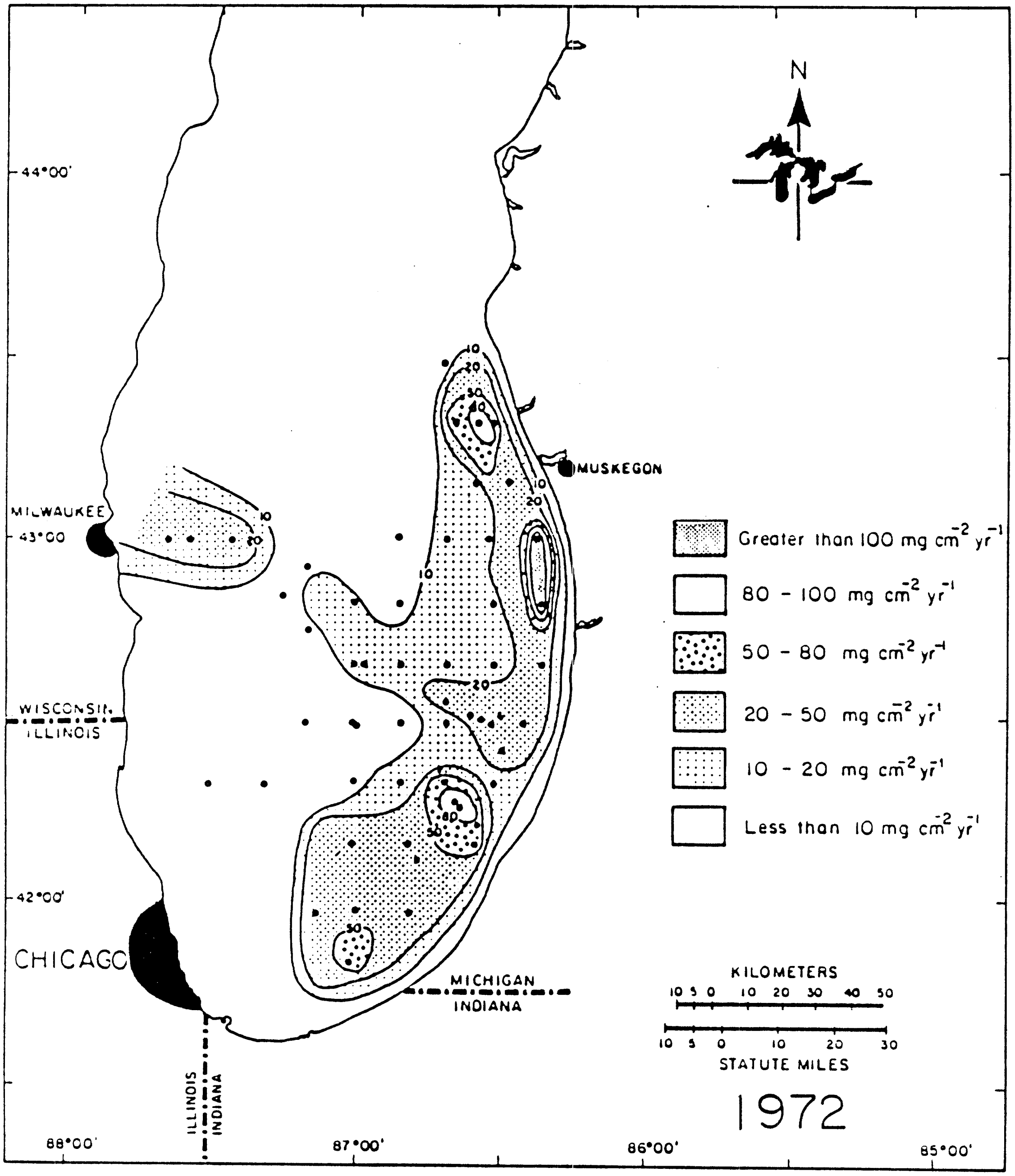

FIG. 8. Sedimentation rate distribution in southern Lake Michigan determined from sediment cores collected in 1972 (from Benante 1984).

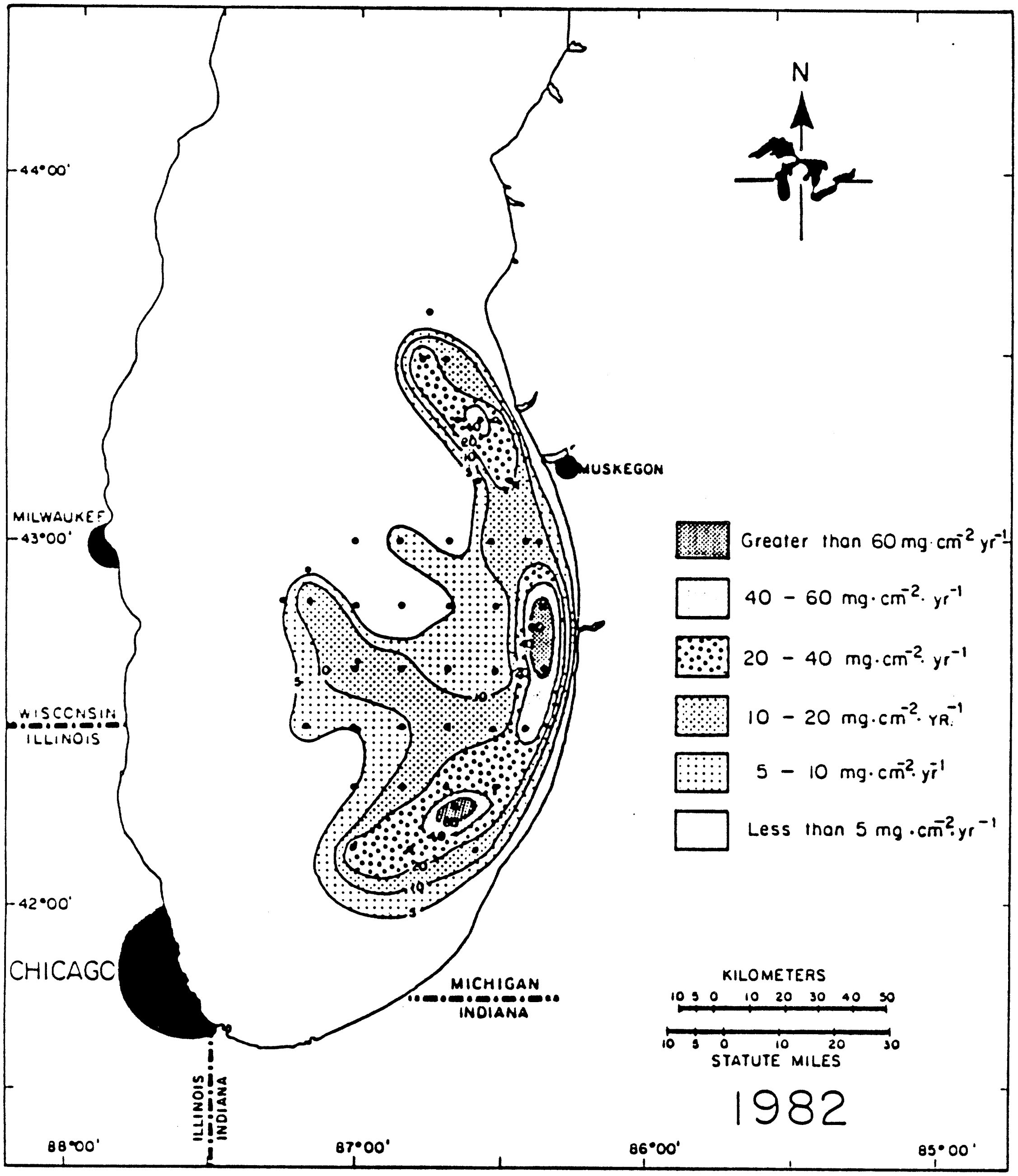

FIG. 9. Sedimentation rate distribution in southern Lake Michigan determined from sediment cores collected ten years later in 1982 (from Benante 1984).

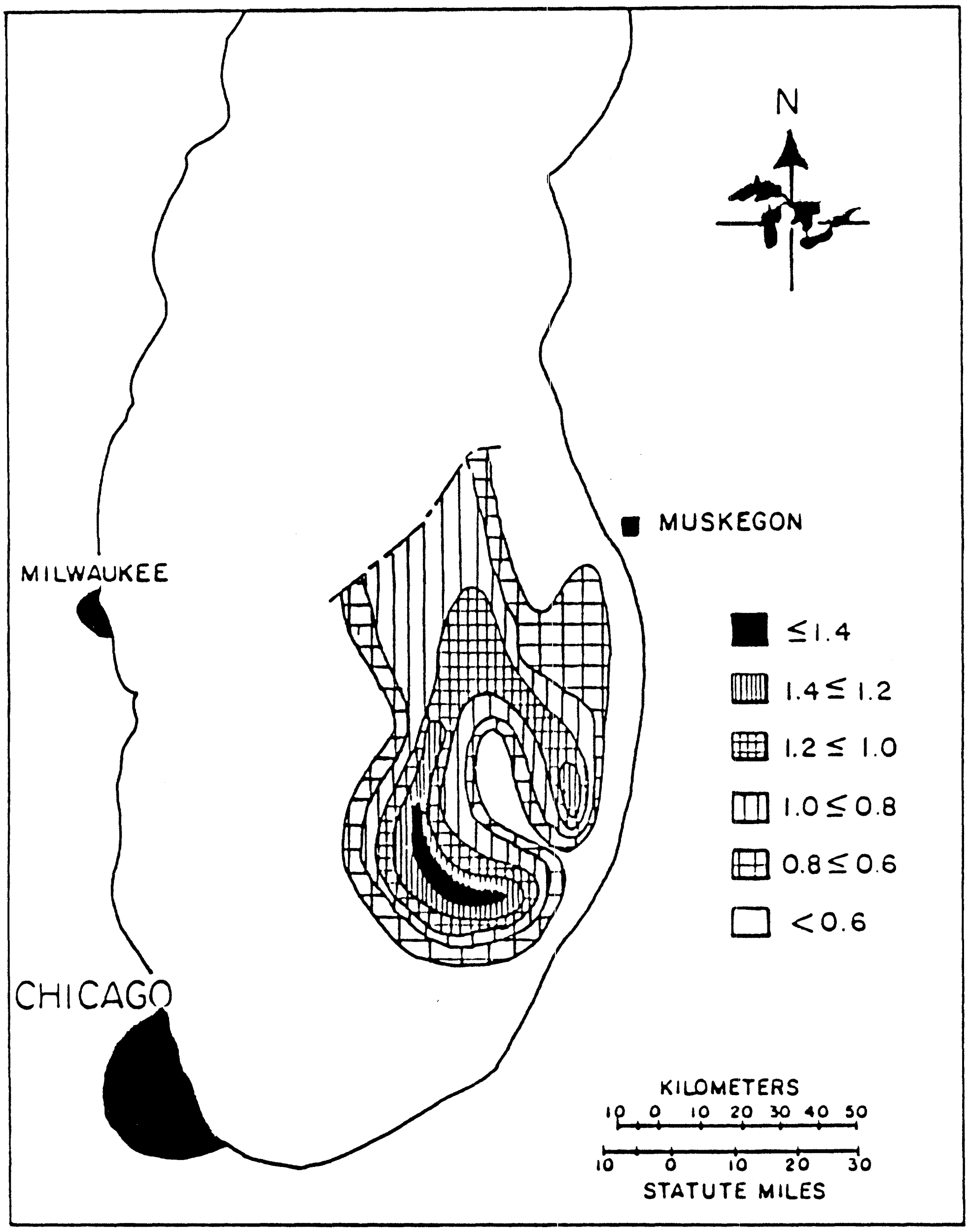

FIG. 10. The relative distribution of Cs-137 in southern Lake Michigan between 1972 and 1982. Plotted are the ratios of the 1982 to 1972 total Cs-137 inventories (from Benante 1984). Cs-137 containing sediment has apparently migrated from areas where this ratio is less than 1.0 to areas where it is greater than 1.0. The total mass of Cs-137 in these sediments has not changed, it has only been "refocused" by relatively large-scale resuspension and transport processes.

culation pattern in the lake (Mortimer 1987). Resuspension and circulation apparently combine to transport sediments horizontally over significant distances on a time scale of years. This non-steady-state behavior of the sedimentary sink complicates both sedimentation rate estimates and mass balance calculations which rely on site specific flux and accumulation rates. This type of large scale sediment redistribution is a limnological phenomenon which is probably unique to large lakes but may be common to coastal marine environments.

BENTHIC BIOGEOCHEMICAL PROCESSES

The role of sediments as ultimate sinks in the geochemical cycles of aquatic systems has long been recognized (Borodovskiy 1965; Mortimer 1941, 1942). The role of sediments as processors of deposited material has recently received more attention as investigations have focused on the extent, timing, and manner in which sediments acquire, recycle, and bury material. Inputs to sediments are controlled largely by the physical regimes of water and sediment transport as coupled to the material loading to the system as a whole. Two of the major controls on the function of sediments in biogeochemical cycles are the rate of input and the nature and content of the organic matter in the deposited material.

Organic matter cycling by sediments is important for several reasons, first and foremost because of its effect on the cycling of biolimiting nutrients and oxygen and the importance of the benthic-pelagic coupling in biological food chains. However, the diagenesis and cycling of organic matter in sediments directly affects the biogeochemical cycles of a host of other elements as well. Numerous studies have demonstrated that the chemistry of organic-rich sediments is controlled by a sequence of microbially-mediated respiration and fermentation processes beginning with aerobic respiration and proceeding through a series of anaerobic modes of respiration wherein alternative electron acceptors such as dissolved NO_3^-, solid phase Mn and Fe oxides, and dissolved SO_4^{2-} are sequentially utilized for the oxidation of metabolizable organic matter (Froelich et al. 1979). Generalized schemes of the relationships between microbially-mediated organic matter degradation, pore water chemistry, and sediment-water exchange processes for the C-H-N-O-S-P-Fe-Mn system are shown in Figures 11 and 12. The rate and nature of organic matter decomposition are important components in determining the redox conditions of sediments (i.e., their chemical state) and in determining the nature of the benthic community (i.e., their biological state). Both are important to chemical cycling in sediments. Redox conditions may control the solubility and distribution of chemical substances between sediments and water. Benthic organisms influence, through sediment mixing and irrigation, the distribution of particles in the upper few centimeters of sediment as well as the rate at which pore fluids are exchanged with the overlying water.

Supply of Organic Matter to the Benthic Environment: Natural Gradients

Organic matter loading is probably the most important parameter in determining the role sediments play in the biogeochemical cycles of aquatic systems. The supply of organic matter to the lake bottom may derive from terrestrial, littoral, and pelagic sources. In depositional environments in the Great Lakes this loading varies by 2 to 3 orders of magnitude from

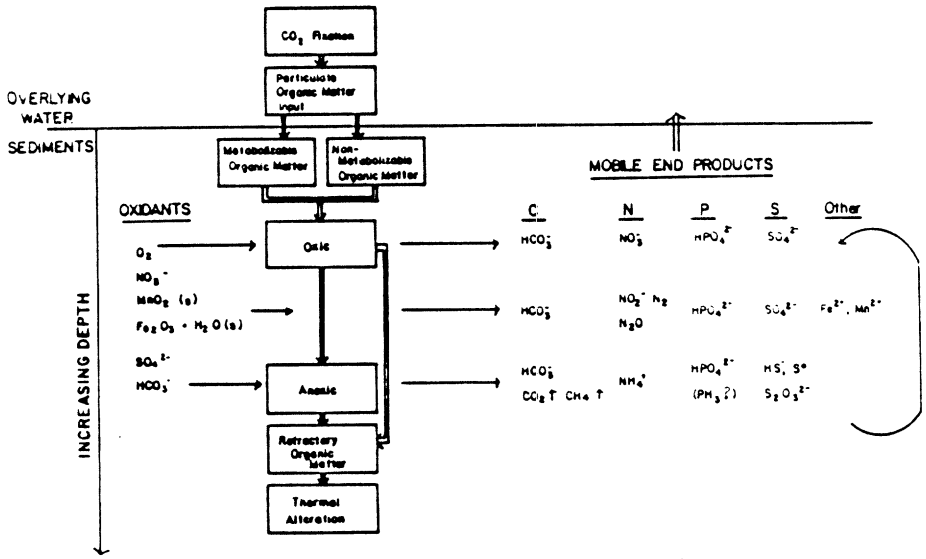

FIG. 11. Schematic diagram of biogeochemical processes associated with the microbially-mediated degradation of metabolizable organic matter in organic-rich sediments (from Martens 1982).

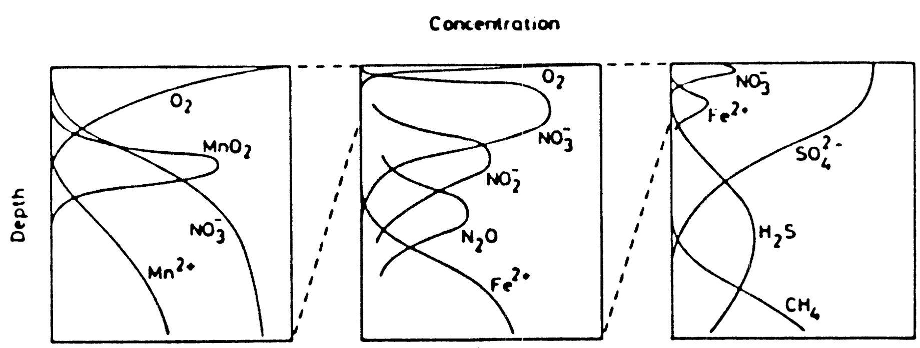

FIG. 12. Schematic distribution of oxidants and their products in the pore waters of aquatic sediments. Because the chemical species differ more than 100-fold in the depth of their distributions, they are shown in three graphs which have different, relative depth scales as indicated by the broken lines. The absolute values of depths and concentrations will depend on the sediment type (from Jorgensen 1983).

less than 0.5 mol C m^{-2} y^{-1} in oligotrophic Lake Superior (Johnson et al. 1982) to greater than 15 moles carbon m^{-2} $year^{-1}$ in eutrophic Green Bay (Klump et al. unpub. data). In the ocean, the fraction of the organic matter fixed within the photic zone actually deposited on the seafloor is most directly related to water depth (Fig. 13; Suess 1980). The deeper the water, the longer the transit time from the photic zone to the bottom. Degradation within the water column is more complete and the fraction of metabolizable carbon surviving remineralization and reaching the sediment-water interface is small. In the Great Lakes this fraction probably varies from a few percent to over 25% as one moves from the deep upper lake environments to the shallower lower lakes, coastal bays, and estuaries. As a result, the Great Lakes contain a broad range of benthic systems from organic poor environments, which have been compared to hemipelagic and pelagic marine sediments (Johnson et al. 1982), to hypereutrophic organic rich bays. Consequently, the lakes provide a "natural laboratory" of benthic environments in which to study the effect of the so-called "master variable" -- the flux of metabolizable organic substrates to the bottom.

The speed with which this material reaches the lake floor is important. A small fraction of very fresh and rapidly consumed detritus may be a significant energy source for benthos. Fecal pellets and vertically migrating zooplankton may deliver organic-rich materials even to the deepest regions of Lake Superior (>400 meters), where abundant benthic zooplankton-benthos-fish communities have been observed.

Sediment-Water Exchange Processes

In the shallower bays and lakes the proximity of the bottom results in a more rapid transport of material to the sediments. Estimates of particle residence times in the water column based upon Be-7 inventories in Lower Green Bay indicate Be-7 deposition to be on the order of days to weeks. In shallow, productive environments like Green Bay, significant quantities of labile organic matter enter the benthic system. Decomposition processes result in the establishment of steep concentration gradients for remineralized carbon and nitrogen (Fig. 14) and anoxic conditions within mm of the sediment-water interface (Fig. 15). The extent to which deposited organic matter undergoes further decomposition is dependent, in part, on the extent to which remineralization processes have occurred within the water column. In Green Bay it is estimated that between 10% and 40% of the organic carbon and nitrogen deposited at the sediment-water interface is recycled back into the overlying water. Direct measurements of the production of remineralized carbon (CO_2 and CH_4) and nitrogen in incubated sediments indicate that decomposition occurs relatively quickly, i.e., within the upper few cm of the sediment (Fig. 16).

The turnover rate for this recycled component may be estimated from the residence times for metabolizable carbon in the sediment column. In organic rich sediments these residence times are on the order of 2 years. By comparison, in deep Lake Superior sediments, total organic carbon turnover is much slower -- on the order of decades (Johnson et al. 1982).

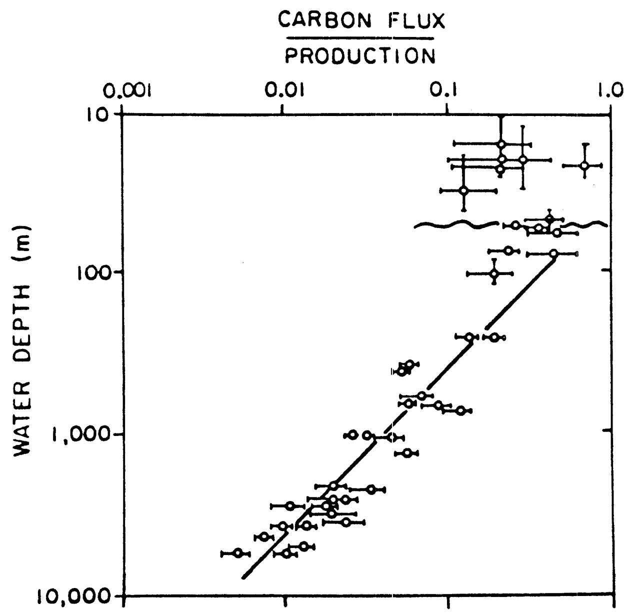

FIG. 13. Organic carbon fluxes with depth in the water column normalized to mean annual primary production rates at the sites of sediment-trap deployments. The linear regression (solid line) is represented by the equation: $C_{flux(z)} = C_{prod}/(0.0238z + 0.212)$ (from Suess 1980).

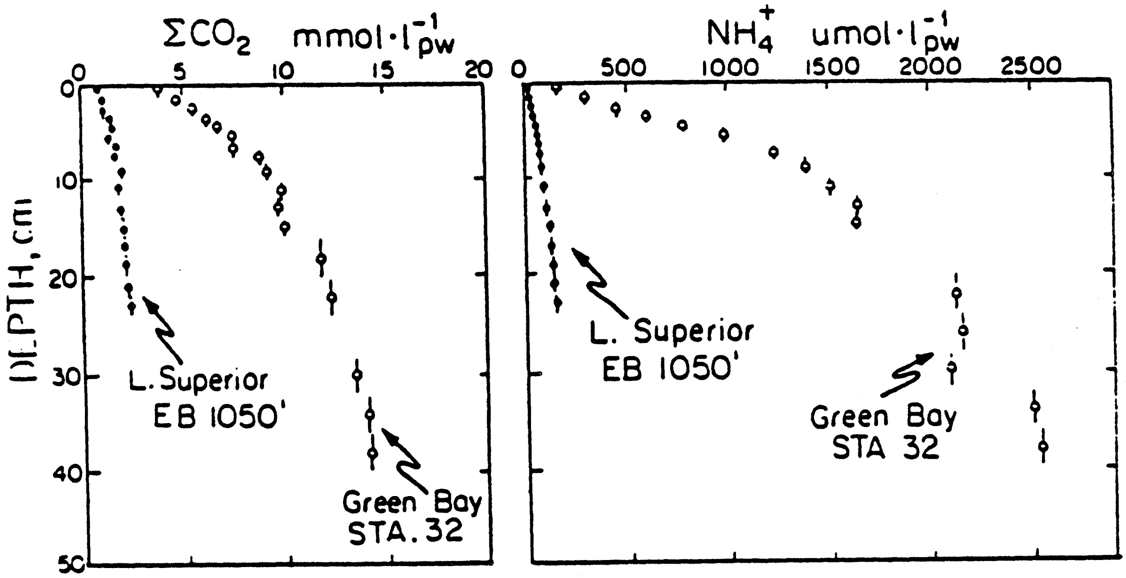

FIG. 14. Pore water profiles for dissolved ammonium and total inorganic carbon in sediments from a deep Lake Superior station and a shallow organic-rich Green Bay station.

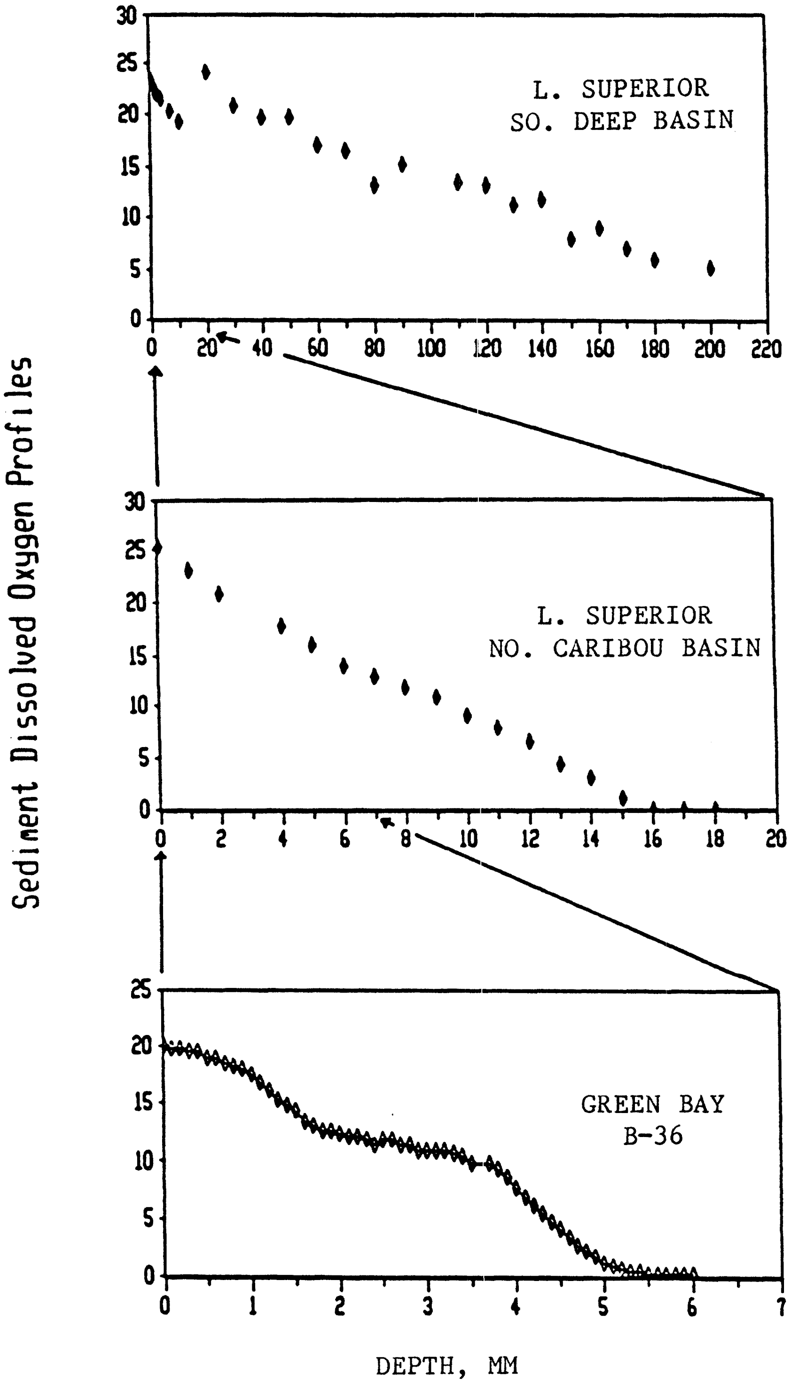

FIG. 15. Dissolved oxygen profiles at three stations in the Great Lakes showing the range in benthic metabolism. Oxygen depletion occurs at depths from mm to tens of cm.

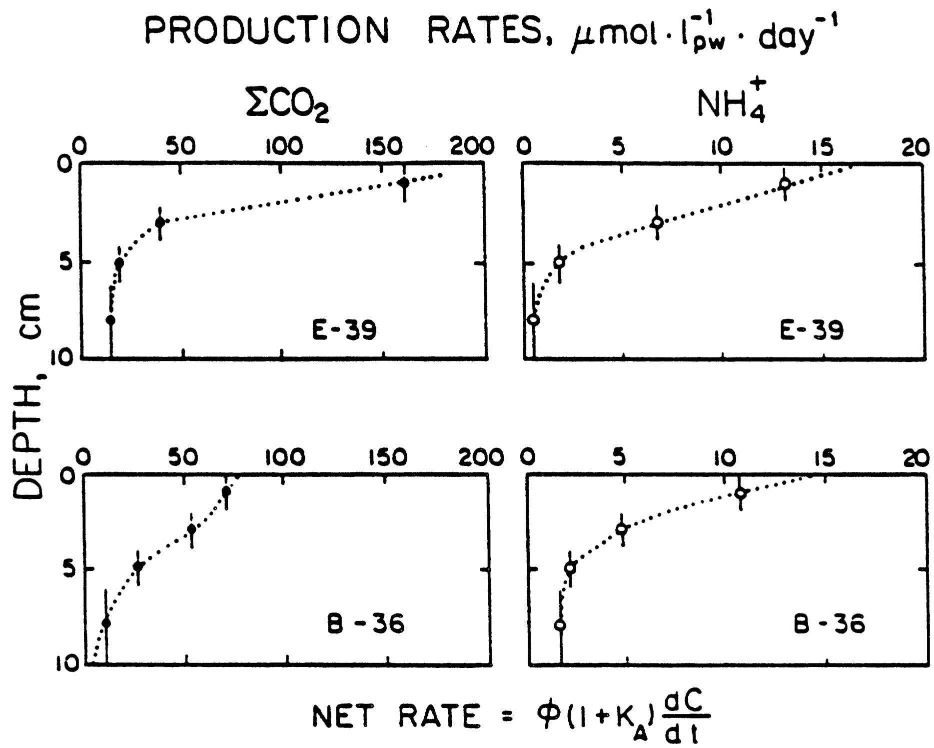

FIG. 16. Carbon and nitrogen anaerobic remineralization rates in the upper 10 cm of two organic-rich stations in Green Bay, Lake Michigan.

A major factor controlling the importance of benthic-pelagic coupling, therefore, appears to be water depth. In this regard the Great Lakes or portions thereof should behave very differently. In general, lake level changes would affect little other than shoreline erosion. However, given the recent upswing in lake levels (as much as 2 meters above record low levels), relative effects on Lakes Michigan and Erie, for example, might be dramatic. Lake Michigan's average depth is 84 meters, Lake Erie's only 17 meters. A meter change in level, while insignificant in the case of Lake Michigan, could result in a significant increase in the volume of the hypolimnion in Lake Erie. Given the sensitivity of sedimentary phosphorus recycling to hypolimnetic oxygen, and the influence of stratification on resuspension of bottom sediments into the epilimnion, lake level changes of this magnitude may be important in the biogeochemical cycles of shallow lakes and bays.

Animal-sediment Interactions

Animal-sediment interactions have several important impacts on benthic biogeochemical processes.

1) Biogenic mixing of sediments tends to homogenize sediment particles accumulated over a period of years forming a "mixed layer" in the upper 3 to 4 cm of sediments (Robbins et al. 1977).

2) Organisms increase the rate of exchange of pore fluids with overlying waters (Krezoski et al. 1984). This, for example, increases the rate of silica dissolution by pumping undersaturated bottom water into surface sediments.

3) Macrofaunal irrigation through burrows and tubes alters the geometry of diffusion in sediments from one of solely vertical movement to one of both horizontal and vertical diffusion (Aller 1980).

4) Tubes and burrows themselves represent microenvironments which are sites of enhanced microbial and meiofaunal activity because of elevated organic contents and gradients of metabolites (Aller 1986).

5) Macrofauna may increase the release of metabolites through the processes of digestion and excretion (Gardner et al. 1981).

6) Deposit feeders can rapidly assimilate organic contaminants, bringing them into a form which maintains them in the biologically active surface layer (Klump et al. 1987).

LAKE-AQUIFER INTERACTIONS

The interactions between lakes and aquifers deserve brief mention. Lakes are not impermeable bowls. Water movement between lakes and their underlying aquifers is important in both the hydrological and geochemical budgets of many small lakes. Recent investigations on groundwater-lake interactions in the Great Lakes have indicated that groundwater contributions to Lake Michigan are potentially significant (Cherkauer 1983). Preliminary calculations yield estimates that the groundwater flux to the lake under the natural lakeward gradient is large (10^5 - 10^6 gal d^{-1} per mile of shoreline) and may be between 4% and 20% of the inflow to the lake from rivers along the Wisconsin shoreline (Rovey 1983, Bradbury 1982).

The geochemical impact of such exchanges is not known. It is clear, however, that in addition to the surface watershed there exists a potentially important subterranean watershed which may have geographic boundaries wider, in some instances, than the surface drainage basin. Groundwater withdrawals, recharge, pollution, etc. both inside and outside the conventional Great Lakes basin may impact the lakes at least locally. A highly unique example of groundwater impacts on a large lake has been recently suggested for Yellowstone Lake, Wyoming, where hydrothermal springs may represent a significant nutrient source for this nitrogen limited, oligotrophic lake (Remsen et al. 1986).

CONCLUSIONS

1. A major characteristic of large lakes is the importance of internal cycling processes relative to allocthonous inputs. An improved understanding of the biogeochemical cycles in the Great Lakes will require a better understanding of nutrient and carbon recycling pathways over both seasonal and annual time scales.
2. The coupling between hydrodynamics and biological/biogeochemical processes in large lakes is unique and important. The hydrodynamics of coastal boundary processes, upwelling phenomena, and onshore-offshore transport processes deserve more attention. Because the scale and complexity of these phenomena are often beyond the practical scope of individual projects, the Great Lakes would benefit from a "CUEA (Coastal Upwelling Ecosystem Analysis) type" program designed to investigate the coupling between hydrodynamics, biology, and biogeochemical cycling.
3. Our basic understanding of mass balances relies heavily on estimates of primary production. The degree of uncertainty in carbon and phosphorus fixation and recycling estimates translate directly to uncertainties in the biogeochemical budgets for these and other elements. Better estimates of annual net primary production are fundamental to our understanding of nearly all aspects of the Great Lakes ecosystem.
4. The physical dynamics of the benthic system, and sediment transport in general are complex and interesting. The concept of a lake as a bowl with sediments steadily accumulating on the bottom is not applicable to large lakes. Seasonal cycles in particle production and removal processes and decade scale sediment refocusing are significant processes affecting the fate of chemical constituents.
5. Environments found within the Laurentian Great Lakes cover a wide spectrum in terms of fundamental variables such as depth, water retention times, productivity, organic matter loading rates, etc. These natural gradients and differences can be exploited to learn more about the biogeochemical controls operable in the ecosystem.

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APPENDIX B3

LAKE-WATERSHED INTERACTIONS: AN OVERVIEW OF THE EFFECTS OF NUTRIENTS ON LAKES

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This review summarizes recent research on the effects of external loading on total phosphorus concentrations in lakes, and on the effects of nutrients and nutrient gradients on phytoplankton, macrophytes, zooplankton, and fish. Areas of research which are particularly relevant to the Laurentian Great Lakes are discussed which I hope will stimulate future studies in the Great Lakes basin.

In the 100 years since Forbes (1887) wrote his historic essay on the lake as a microcosm, we have increasingly appreciated that lakes cannot be considered independently of their watersheds. The hydrological and biological properties of lakes strongly reflect the characteristics of the basins in which they lie. Consequently, the structure, metabolism, biogeochemistry, and particularly the management of a lake cannot be understood without adequate consideration of inputs from its watershed and airshed (Likens 1985). The purpose of this paper is to present a brief overview of our current knowledge of the effects of nutrients and nutrient gradients on lacustrine ecosystems, and to suggest several areas of research which may be of particular interest to those studying the Laurentian Great Lakes.

NUTRIENT LOADING MODELS

Since the pioneering work of Theinemann (1925) and Naumann (1932), we have begun to better understand the links between nutrient inputs from the watershed and airshed (primarily phosphorus and nitrogen) and the nutrient content and productivity of lakes. Numerous early studies demonstrated the effects of domestic drainage on the eutrophication of European and American lakes (cf. Hasler 1947), and nutrient budgets (e.g., Sawyer 1947, Thomas 1957) helped quantify the annual mass loading of phosphorus to lakes (Lp, milligrams P per square meter per year). Sawyer (1947) subsequently was able to correlate the probability of nuisance summer algal blooms with the magnitude of annual phosphorus loading.

It was soon realized, however, that lake trophic state was not related to areal phosphorus income alone, but to the morphometric characteristics of the lake as well. Edmondson (1961) emphasized the importance of finding a common basis with which to compare rates of external nutrient supply, and demonstrated the utility of a graphical method which used annual areal P income (Lp), lake mean depth (z, meters), and the potential concentration

of total phosphorus in the lake (TP, milligrams per cubic meter). A similar approach was used by Vollenweider (1968) in his classic graphical analysis for the prediction of lake trophic state.

Since the publication of Vollenweider's (1968) paper, a great deal of work has focussed on the refinement of input-output phosphorus loading models (cf. Vollenweider and Kerekes 1980; Reckhow and Chapra 1983). Central to these recent models is a term which estimates the fraction of the total phosphorus input which is retained annually by the lake. In the case of Vollenweider's most recent models (OECD 1982), phosphorus retention is approximated by an expression involving the lake hydraulic residence time (tw, years):

$$TP = \frac{Lp\ tw}{z\ (1 + tw^{.5})} \qquad (1)$$

In the Dillon-Rigler (1974) model, phosphorus retention is included explicitly as the phosphorus retention coefficient Rp:

$$TP = \frac{Lp\ (1 - Rp)}{qs} \qquad (2)$$

where qs is the areal water loading to the lake (meters per year). In the case of Eq. 2, however, the phosphorus retention coefficient must be estimated independently (e.g., from equations involving qs; cf. Dillon and Kirchner 1975; Ostrofsky 1978).

Despite these advances, however, we require more detailed knowledge of phosphorus retention if we are to accurately predict the changes in TP which will occur when the external loading is altered. Certainly, one important factor which deserves further study is the effect of varying concentrations in the inflow of rapidly-settling material (Edmondson and Lehman 1981; Chapra 1982; Lehman and Edmondson 1983; Chapra and Reckhow 1983). However, even where the total phosphorus load is predominantly dissolved in nature (and thus most biologically available), we typically presume that phosphorus retention is solely dependent on the hydraulic characteristics of the lake.

As noted by Reckhow and Chapra (1983), this is not a reasonable assumption. Phosphorus retention is dependent upon many other chemical and biological variables, and further research is needed to determine their relative importance. For example, Nürnberg (1984) has developed models accounting for the influence of internal loading on phosphorus retention, but even in lakes with oxic hypolimnia one can expect other factors to influence the net loss of phosphorus from the water column to the sediments.

One such factor which should influence phosphorus retention is the concentration of nitrogen in the water column. The importance of nitrogen in eutrophication has been discussed by Vollenweider (1968, 1975), and nitrogen loading models have subsequently been developed for lakes (e.g.,

Bachmann 1981; OECD 1982). However, the potential effects of nitrogen on the recycling and retention of phosphorus in the water column have received insufficient attention.

Ripl (1976) and Ripl and Lindmark (1978) noted that high concentrations of nitrate in the water overlying phosphorus-rich sediments help decrease the rate of phosphorus release into the water column, and proposed the use of nitrified sewage effluent or nitrate addition as a lake restoration tool. Moreover, in a recent study of 31 eutrophic Danish lakes, Andersen (1982) noted that elevated nitrate concentrations in the overlying water (>ca. 0.5 - 1 grams N per cubic meter) prevented phosphorus release from the sediments in stratified lakes with anoxic hypolimnia, and in shallow polymictic lakes with well-oxygenated water. These observations suggest that the magnitude of nitrogen loading should have a pronounced effect on net phosphorus sedimentation and retention, and should be included in future models predicting the concentrations of total phosphorus in oxic lakes (Smith and Prairie, in prep.).

Such effects on phosphorus retention should be particularly evident in embayments of the Great Lakes which exhibit marked horizontal concentration gradients of both nitrogen and phosphorus. An analysis of phosphorus mass balance in defined segments of such embayments (e.g., Saginaw Bay, Lake Huron: Bierman and Dolan 1980; Bierman et al. 1984) with this hypothesis in mind would be valuable. In addition, this hypothesis could be directly tested in Lake Superior, which has experienced exponential increases in nitrogen loading during the past several decades (Bennett 1986).

NUTRIENT EFFECTS ON ALGAL BIOMASS

Although it was clear to early researchers that summer blooms of algae were dependent on the fertility of the lake water, it was not until the seminal work of Sakamoto (1966) that the correlation between summer chlorophyll and nutrients in the water column was adequately quantified. Numerous investigators (e.g., Dillon and Rigler 1974; Vollenweider 1976; Jones and Bachmann 1976) subsequently developed further phosphorus-chlorophyll models for lakes, and these models have been further modified by the inclusion of total nitrogen as an additional predictive variable (Smith 1982; Canfield 1983). However, the residual scatter in all such models is considerable, and we still have much more to learn about the factors which modify the amount of algal biomass produced at given concentrations of nitrogen and phosphorus.

Lake depth and its effect on average subsurface light availability is one such factor which has not been given sufficient attention since its discussion by Talling (1971). Ramberg (1978) and Ahl (1980), for example, observed an apparent decrease in algal biomass at a given concentration of total phosphorus in deep Swedish lakes relative to more shallow lakes. Pridmore et al. (1985) have recently developed an empirical model for chlorophyll in New Zealand lakes which explicitly considers lake mean depth and total phosphorus concentration, and the predictions of their model are illustrated in Figure 1. Similar effects of depth on the response of algal biomass to nutrients in the Great Lakes should be examined, especially in embayments versus open water areas, and in the subbasins of Lake Erie.

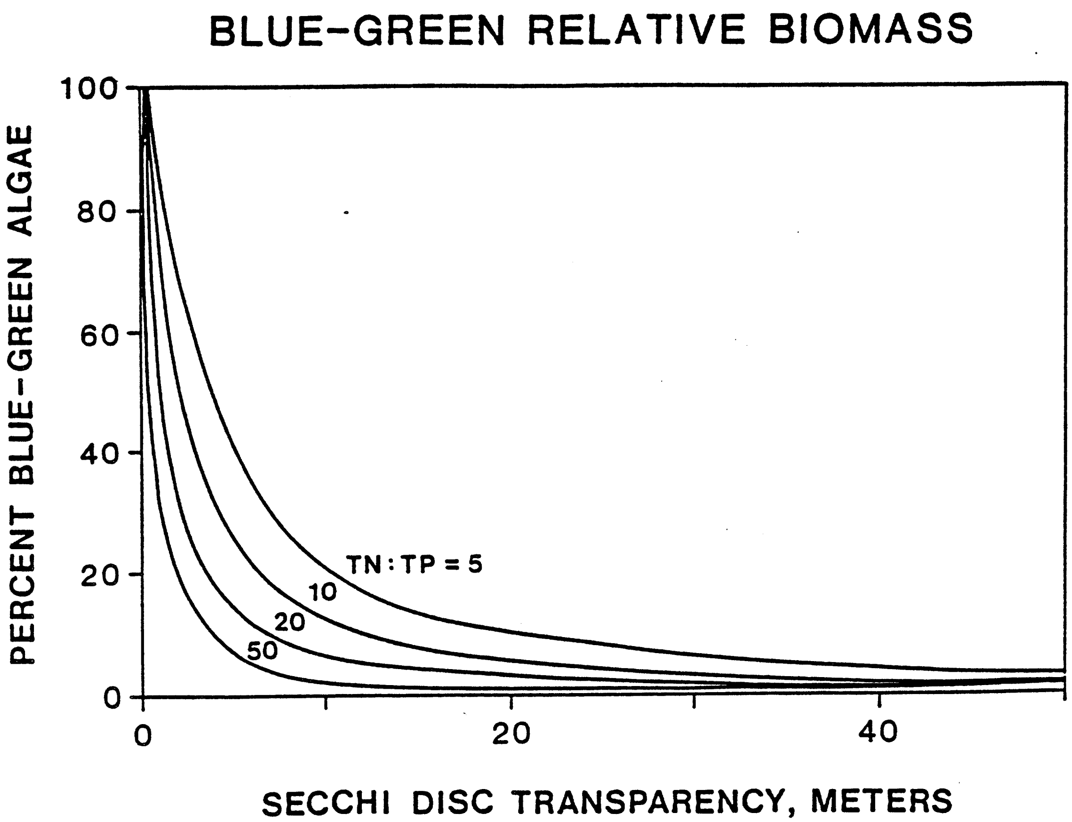

FIG. 1. Effects of lake mean depth on chlorophyll a in lakes (calculated from Eq. 3 in Pridmore et al. 1985).

EFFECTS OF NUTRIENTS ON ALGAL SPECIES COMPOSITION

Although we have a reasonably good understanding of the factors which determine the summer chlorophyll concentration in lakes, we still have only a rudimentary understanding of the factors which determine phytoplankton species composition and succession. Clearly, many factors are involved (cf. Kalff and Knoechel 1978; Harris 1986; Reynolds 1984; Sommer et al. 1986), but whole-lake fertilization experiments (cf. Schindler 1977; Flett et al. 1980; Kilham and Kilham 1984) have demonstrated that changes in nutrient loading can have profound effects on phytoplankton community structure.

One model proposed to explain these changes is based on resource competition theory (Tilman 1977, 1982; Tilman et al. 1982). This theory suggests that the concentrations and ratios of N, P, and Si in the nutrient supply, and the availability of light in the water column, are important determinants of algal species composition. Laboratory competition experiments (Tilman and Kiesling 1984; Tilman et al. 1986) have demonstrated the effects of varying silicon:phosphorus and nitrogen:phosphorus ratios on the species composition of mixed natural algal communities. In general, such laboratory experiments suggest that under conditions of phosphorus limitation (high N:P and Si:P ratios), diatoms should be dominant. Under conditions of silicon limitation (low Si:P ratios), experiments with mixed natural communities suggest that green algae are the most likely dominant. Finally, under conditions of nitrogen limitation (low N:P ratios), blue-green algae should be dominant.

The hypothesis that blue-green algae should be dominant in lakes having low N:P ratios was tested experimentally by Schindler (1977) and Flett et al. (1980), and empirically by Smith (1983a,b). Although the results of these studies were consistent with this hypothesis, as further data became available (Fig. 2) it became increasingly clear that while the epilimnetic total nitrogen:total phosphorus (TN:TP) ratio influenced the relative biomass of blue-green algae, other factors were also important. Consistent with experimental evidence by Zevenboom and Mur (1980), an analysis of these data suggested that light availability, as estimated from Secchi disk transparency (SD, meters) and the mixed depth (Zm, meters), must be considered (Smith 1986):

$$\begin{aligned} \text{logit } (\%\text{BG}) = 2.358 - 1.297 \log \text{TN} + 0.692 \log \text{TP} \\ - 2.058 \log \text{SD} + 0.538 \log \text{Zm}. \end{aligned} \quad (3)$$

The predictions of this model are shown in Figure 3 for a hypothetical lake having a mixed depth of 10 m. An additional factor not included in Smith's (1986) analysis, but which should be considered in the case of the Great Lakes, is that of temperature. Tilman et al. (1986) found strong effects of temperature on the dominance of blue-green algae in natural community chemostats -- blue-greens dominated at all N:P ratios less than 20:1 (by moles) at 24°C, but were not dominant at any N:P ratio at either 10°C or 17°C. Furthermore, McQueen and Lean (1987) have found a marked influence of temperature on the dominance of blue-green algae in Lake St. George, Ontario. These two studies suggest that even given identical concentrations and ratios of TN and TP, the deeper, colder areas of the Great

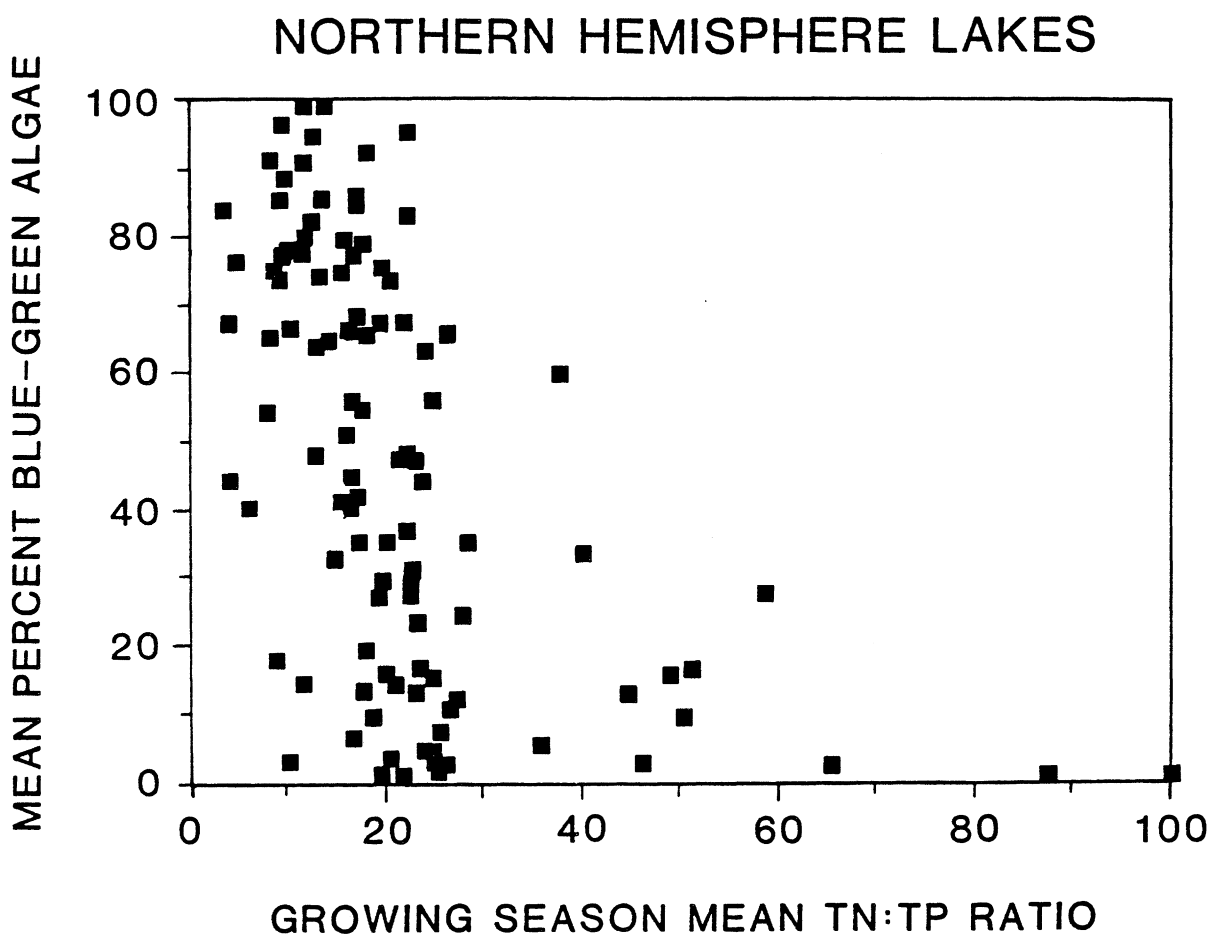

FIG. 2. Relationship between the growing season mean proportion of blue-green algae and epilimnetic TN:TP ratios in 22 northern hemisphere lakes.

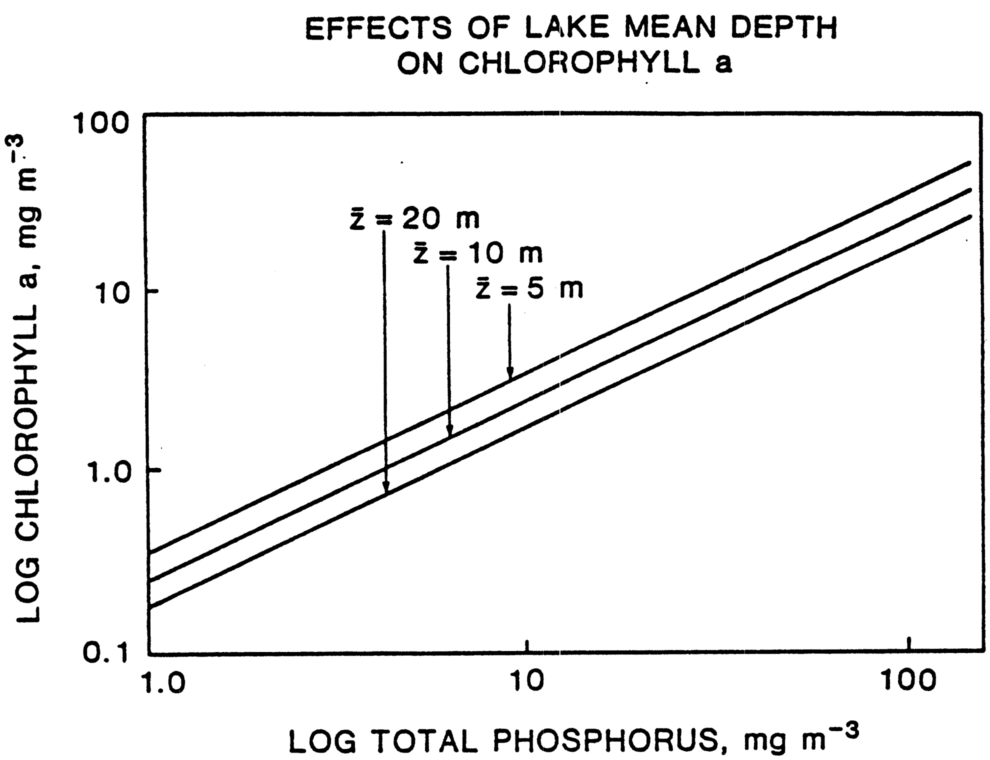

FIG. 3. Graphical presentation of the predictions of Eq. 3 for a hypothetical lake having a mean depth of 10 meters.

Lakes should be less likely to exhibit blue-green algal dominance than the warmer embayments.

Although the relative biomass of different taxa is of ecological interest, it is often the absolute biomass of nuisance algal species which is often of more practical importance. In an analysis of data from the large lakes of Sweden, Smith et al. (1987) have developed models to predict the summer peak biomass of four species of blue-green algae which are potentially capable of producing toxins (Carmichael 1986): (*Aphanizomenon flos-aquae*, *Anabaena flos-aquae*, *Oscillatoria agardhii*, and *Microcystis aeruginosa*). Similar models for individual nuisance species could also prove to be of value in the Great Lakes.

EFFECTS OF NUTRIENT LOADING ON VEGETATION COVER

Another important question in aquatic ecology is the degree to which nutrient loading influences the growth of macrophytes and nearshore vegetation in lakes. Recent independent studies by Duarte et al. (1986) and Smith and Wallsten (1986) have quantified the relationship between lake morphometry and the areal cover of macrophytes. However, for lakes of similar morphometry, there is frequently considerable variation in the observed amount of vegetation cover. Current theory (cf. Wetzel 1983, Figs. 19-10) and experimental evidence (e.g., Boyd and Hess 1970; Boyd and Walley 1972; Zdanowski et al. 1975; Granéli 1985; Anderson and Kalff 1986) suggests that nutrients may in part be responsible.

This hypothesis has been tested empirically in Swedish lakes by Smith and Wallsten (1986), who found that the areal cover of emergent macrophytes (EMERGE, hectares) and of floating-leaved macrophytes (FLOAT, hectares) appeared to be dependent on the concentration of total nitrogen (TN, milligrams per cubic meter) in the water column, lake surface area (AREA, square kilometers), and on lake mean depth (z, meters):

$$\log \text{EMERGE} = -1.853 + 1.102 \log \text{AREA} - 0.586 \log z + 1.071 \log \text{TN} \quad (4)$$

$$\log \text{FLOAT} = -2.390 + 1.151 \log \text{AREA} - 1.117 \log z + 1.266 \log \text{TN}. \quad (5)$$

In contrast, trends in the biomass of submerged macrophytes in Scottish lochs (Harper 1986) show very different patterns when plotted versus total nitrogen and total phosphorus (Figs. 4-5). Furthermore, data from Dutch ponds and pools suggest that phosphorus is more important than nitrogen for nitrophilous dune hemicryptophytes growing on more sandy substrates (Meltzer and van Dijk 1986) (Fig. 6). These data underscore the need for critical investigations of growth-limiting factors for macrophytes and nearshore vegetation in lakes, and their responses to changes in external nutrient loading. Comparative studies of the Laurentian Great Lakes similar to those made of macrophytes in the large lakes of Sweden (e.g., Andersson 1978) would provide valuable data which could be used to develop models for the Great Lakes.

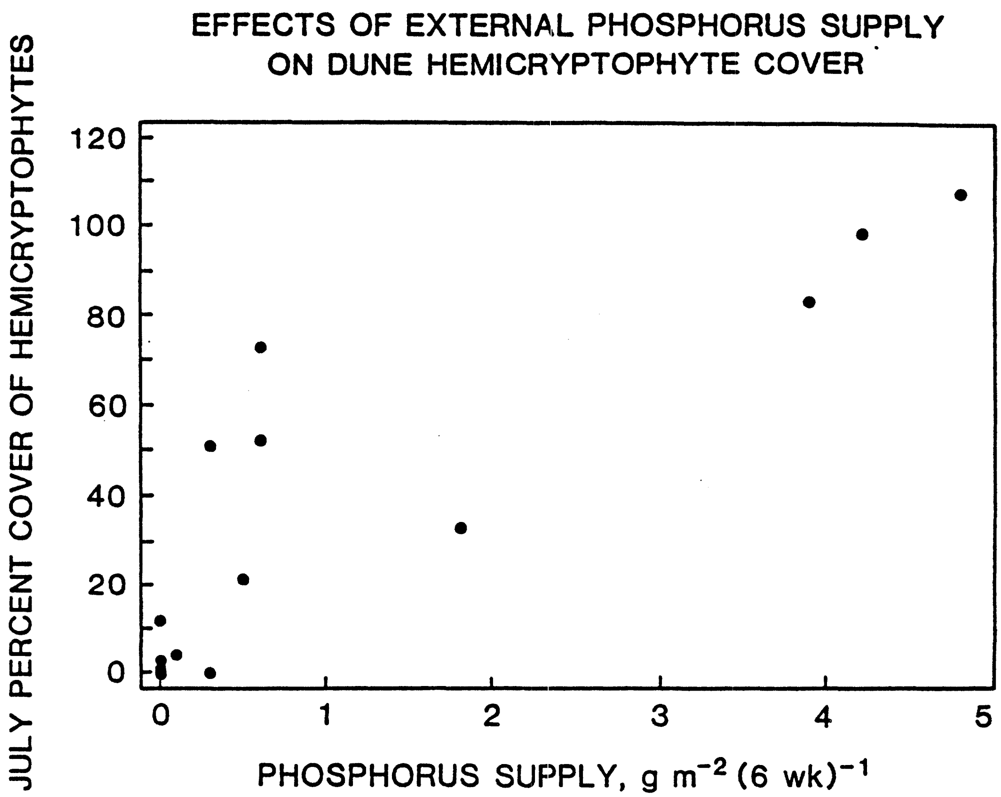

FIG. 4. Relationship between nitrophilous hemicryptophyte cover and external phosphorus supply to Dutch dunes (data from Meltzer and van Dijk 1986).

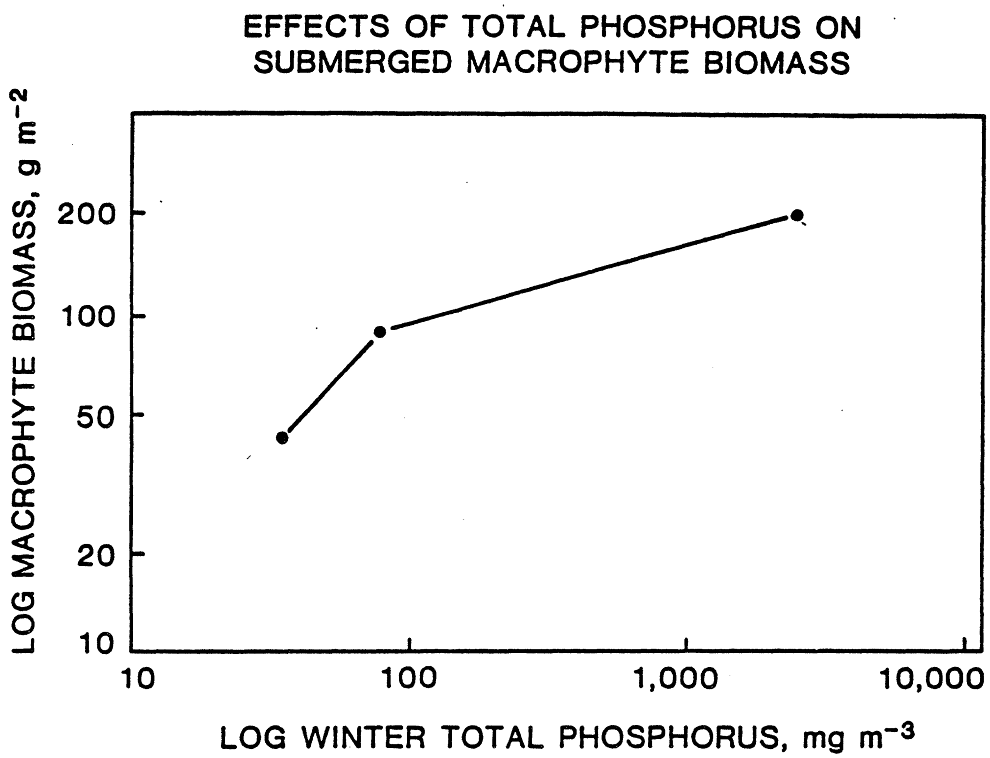

FIG. 5. Relationship between submerged macrophyte biomass and total phosphorus concentrations in three Scottish lochs (data from Harper 1986).

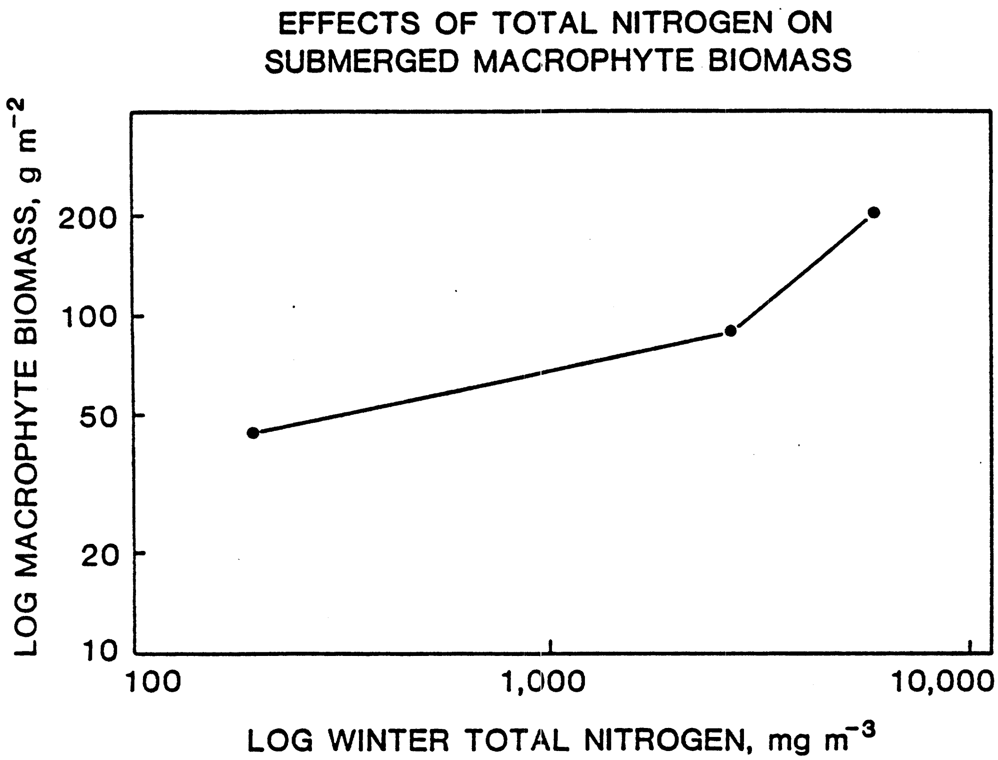

FIG. 6. Relationship between submerged macrophyte biomass and total nitrogen concentrations in three Scottish lochs (data from Harper 1986).

EFFECTS OF NUTRIENTS ON ZOOPLANKTON AND BENTHOS POPULATIONS

As can be predicted from current theories of trophic dynamics, the biomass of zooplankton in lakes strongly dependent on lake primary production (Brylinsky 1980; McCauley and Kalff 1981). However, the question of food quality effects on zooplankton feeding and growth in lakes is receiving increasing attention (e.g., Gliwicz 1980; Infante and Edmondson 1985; DeMott 1986). As discussed earlier, the supply ratios of nutrients to lakes should have important effects on the phytoplankton species composition. To the extent that these changes in algal species composition result in changes in the growth rates of herbivores (e.g., Infante and Litt 1985), changing nutrient supply ratios should alter the biomass of zooplankton produced at a given concentration of total phosphorus.

In addition to these changes in community structure, the biochemical composition of the phytoplankton should also respond to changes in nutrient loading to the lake. For example, chemostat studies (e.g., Rhee 1978; Rhee and Gotham 1981) have shown that the biochemical composition of algal cells is dependent on the N:P supply ratio and light availability, and in a recent comparative study of the nutrient content of lake seston, Harris (1986) found marked differences in seston P:C ratios in lakes of different trophic state. Harris did not find similar trends in seston N:C ratios, but Aizaki et al. (1986) observed marked variations in the seston N:C ratio in outdoor ponds exposed to different levels of phosphorus loading (Fig. 7). If this biochemical variability in turn influences the nutritional value of the seston, one can expect consequent changes in the growth efficiency of herbivores. For example, in his recent review Mattson (1980) showed that the growth efficiency (mg body growth per mg food ingested) of herbivores is dependent on the nitrogen content of their food, and Ambler (1986) has subsequently demonstrated the effects of algal N:C ratios on the in situ specific egg production rate of the marine copepod, *Acartia tonsa* (Fig. 8).

It is important to note that the N:C ratios at which Ambler (1986) observed these effects lie within the range of variability noted by Aizaki et al. (1986). Furthermore, since food nitrogen content can also influence the growth rate of marine deposit feeders (Tenore 1983; Tenore and Chesney 1985; cf. Fig. 9), altered seston food quality may also affect benthic consumers in lakes as well. Similar effects of variations in phytoplankton community structure and biochemical composition on the growth of primary consumers may be evident in the Great Lakes. Empirical and experimental investigations of in situ nutrient gradients would be a helpful step in understanding the effects of these gradients on the ecology of zooplankton and zoobenthos in the Great Lakes.

EFFECTS OF NUTRIENTS ON FISH POPULATIONS

As in the case of phytoplankton, both the concentration of total phosphorus (Hanson and Leggett 1982; Lang and Lang 1983) and lake mean depth (Rawson 1952; Ryder 1982) have a strong influence on the biomass and yield of fish, but considerable scatter is evident in these empirical relation-

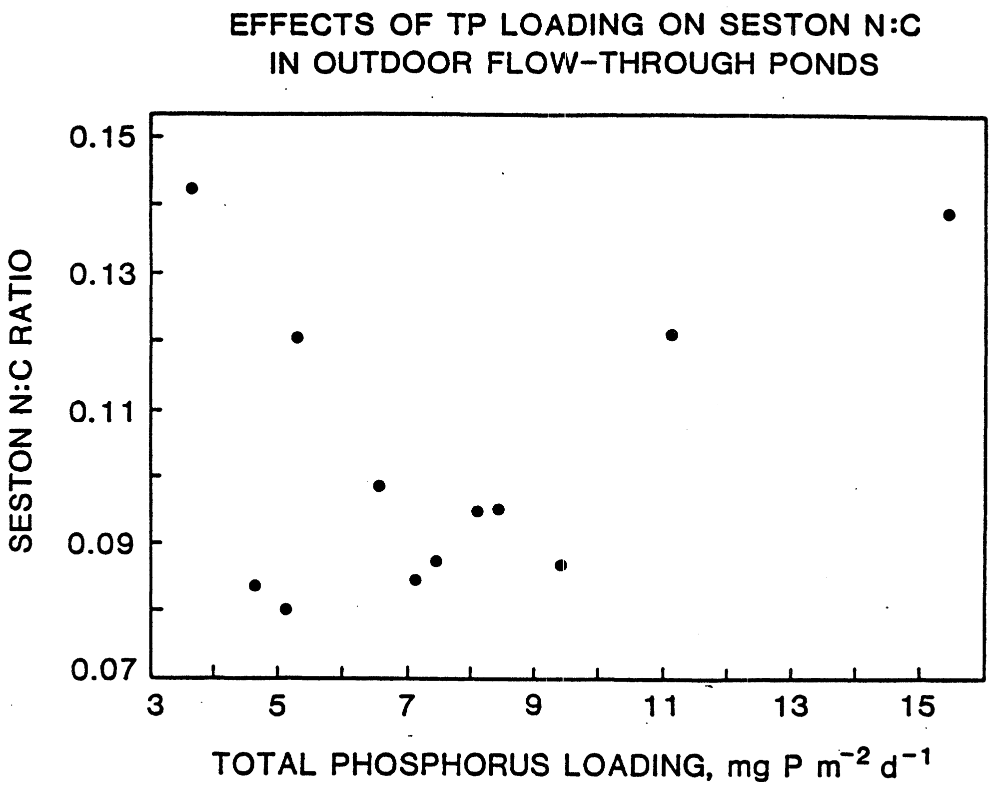

FIG. 7. Observed variation in average seston N:C ratios in continuous flow outdoor ponds exposed to varying levels of phosphorus loading. Note: the inflow N:P ratio to these ponds was held constant at 7:1 by weight (data from Aizaki et al. 1986).

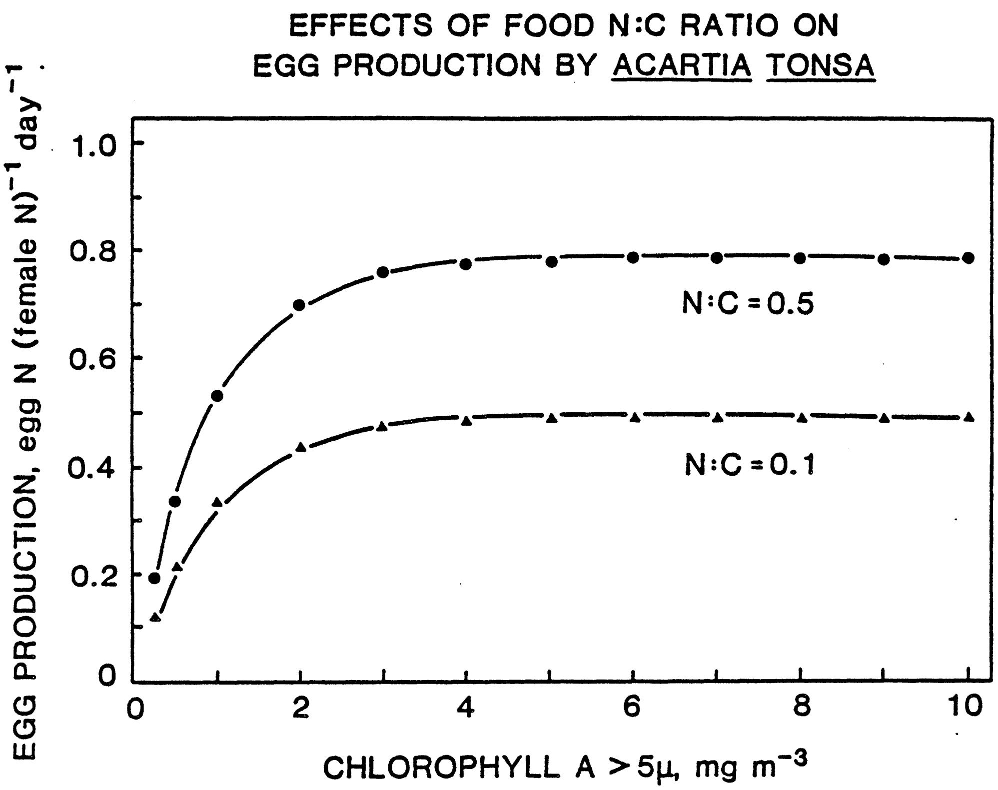

FIG. 8. Effects of food N:C ratios on egg production by Acartia tonsa Dana. Calculated from Eq. 7 in Ambler (1986), assuming a temperature of 20°C and salinity of 20°o/oo.

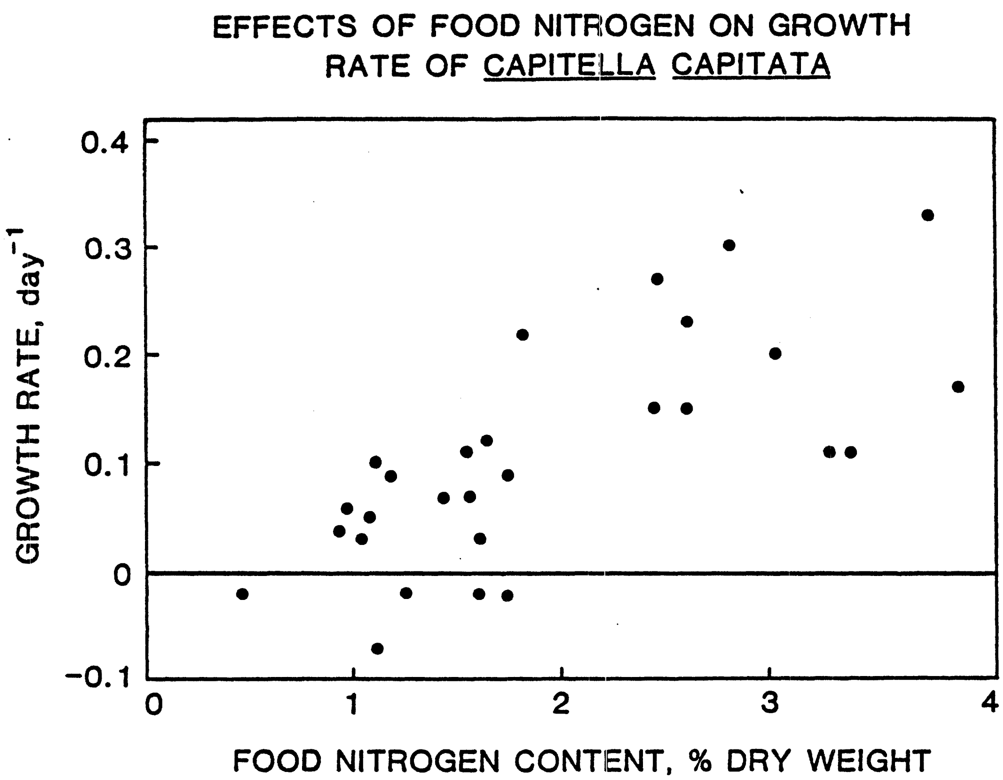

FIG. 9. Effects of food N:C ratios on the growth rate of the marine deposit feeder, Capitella capitata (data from Tenore 1983).

ships. Some of this variance undoubtedly results in part from measurement error, and particularly from the errors inherent in fish biomass or yield estimates. However, it is not unreasonable to assume that some of the residual variance is also biological in nature -- and due, in part, to the effects of other nutrients such as nitrogen. Based on recent studies demonstrating the effects of nitrogen and phosphorus on algal biomass (Smith 1979, 1982; Canfield 1983; Canfield et al. 1985), I suggest that the N:P ratio should in turn directly influence the production of fish from a given concentration of total phosphorus by altering the total amount of primary production potentially available for consumers.

However, resource ratios could also influence fish populations in another way. Analyses of fish production and yield have shown order-of-magnitude differences among lakes in the efficiency of energy transfer from primary producers to fish (cf. Fig. 6.10 in Morgan 1980). These differences must in part be due to variations in the quality of the phytoplankton as food for consumers. The observed influence of N:P ratios on the dominance of blue-green algae (Schindler 1977; Smith 1986), and thus on the portion of primary production channeled into less grazeable algal species (Porter and Orcutt 1980; Infante and Abella 1985), should therefore result in additional effects on the growth of fish populations.

Data from Wróbel (1971) support the hypothesis that N:P supply ratios can alter the productivity of fish populations in experimental ponds (Fig. 10). However, the extent to which N:P supply ratios influence fish production in large lakes is not yet known. The potential effects of changes in water quality on fisheries are an important issue in the Great Lakes Basin (Sullivan et al. 1981), and an examination of the effects of increased nitrogen loading (Bennett 1986) and changing N:P loading ratios on total commercial fish catches from Lake Superior would be of interest.

CONCLUSIONS

In this brief overview, I have attempted to synthesize recent information on the effects of nitrogen loading on the concentrations of total phosphorus in lakes, and research on the effects of nutrients and nutrient gradients on phytoplankton, macrophytes, zooplankton, and fish. I have also proposed questions which I think will be of particular interest to limnologists and ecologists in the Great Lakes basin, and hope that this review will stimulate further research which will increase our understanding of the interactions between lakes and their watersheds.

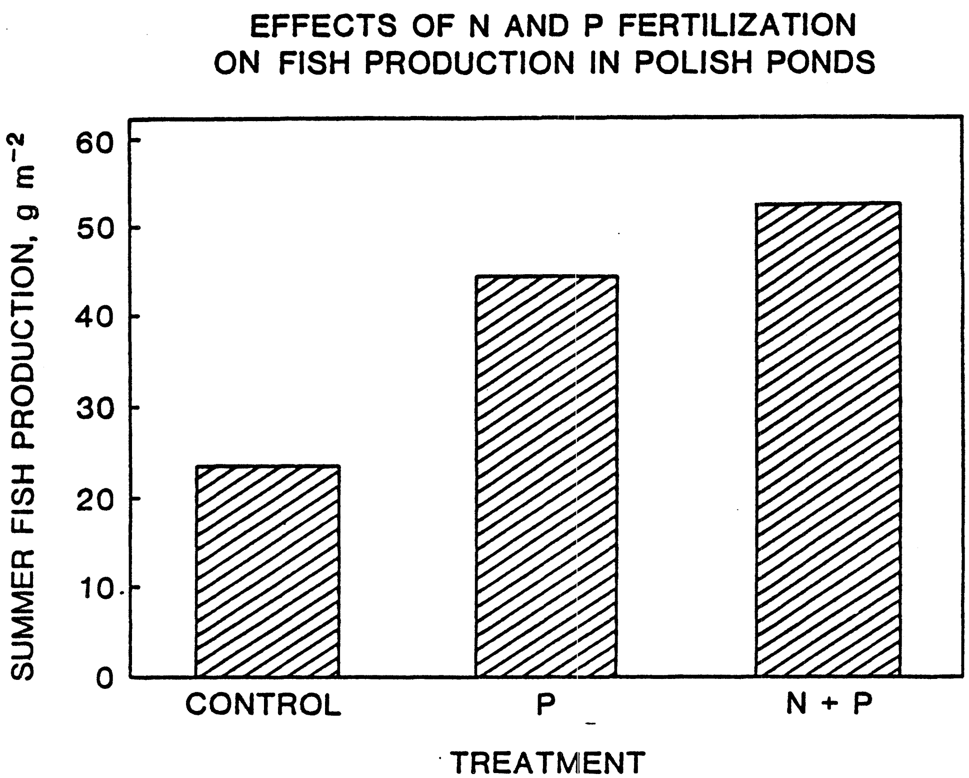

FIG. 10. Effects of N and P fertilization on fish production in Polish ponds (data from Wróbel 1971).

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APPENDIX B4

ANALYSIS OF TEMPORALLY VARIABLE PROCESSES IN LAKE ECOSYSTEMS

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The magnitude of temporal variability exhibited by lake ecosystems continues to surprise limnologists and defy prediction (Edmondson 1979). Paradoxically, management practices intended to maximize fishery yields enhance variability at all trophic levels (Carpenter and Kitchell 1987). While such variability poses significant challenges for aquatic ecologists, it may be essential for the functioning of aquatic communities. Most pelagic food webs would be energetically impossible if predators had to subsist on mean densities of prey, rather than on abundance peaks of variable prey populations (Steele 1984).

Primary production is one well-studied example of a highly variable ecosystem process (Harris 1980, Carpenter and Kitchell 1987). Over the past several years, we have developed a theoretical and experimental approach for analyzing the variability of primary productivity. In this paper, we offer some general comments on the analysis of complex, variable ecological processes, based on our experiences with the effects of food web structure on primary production.

CASCADING TROPHIC INTERACTIONS

A substantial portion of the observed variability in primary production cannot be explained by nutrient supply (Harris 1980; Carpenter and Kitchell 1984, 1987). The cascading trophic interactions hypothesis (Carpenter et al. 1985) proposes that variability in fish community structure resonates through the food web, causing variability in the zooplankton and phytoplankton which leads to variation in primary production that is independent of nutrient loading. Thus, nutrient supply sets the potential primary production, while food web processes cause deviations from that potential.

Temporal variance in fish populations is generally larger than the observed variation in primary production, and therefore potentially large enough to explain the observed variation in primary production (Carpenter

and Kitchell 1987). Fish recruitment is highly stochastic (Pitcher and Hart 1984). For example, ratios of high:low year classes in percids range from 10 to 400 (Koonce et al. 1977), and those for largemouth bass are as large as 2,000 (Summerfelt 1975). Large cohorts affect food web interactions for the lifetime of the fishes. These food web effects vary temporally as fishes grow and feed on progressively larger prey (trophic ontogency; Werner and Gilliam 1984). Large cohos create "predatory inertia" in the system (Stewart et al. 1981), and generate variable numbers of recruits which in turn undergo trophic ontogeny.

The "top-down" perspective did not originate with the cascading trophic interactions hypothesis. Control of community structure by predators is well-known to community ecologists (Kerfoot and Sih 1986), and in fact the "cascade" metaphor comes from studies of predation in intertidal marine communities (Paine 1980). Ecosystem ecology, on the other hand, has been dominated by Lindeman's (1942) model of organic energy flow up the food web (Reiners 1986). The new contribution of cascading trophic interactions was the use of principles from community ecology to explain variation in an ecosystem process, thereby combining "top-down" and "bottom-up" mechanisms in a hierarchical fashion.

MODELS AND EXPECTATIONS

Conclusions of ecological studies are often a function of the time scale of the experiment or sampling regime (Harris 1980; Allen et al. 1984). Because food web dynamics in lakes are variable on a great range of scales (Carpenter et al. 1985), time scale effects are likely to be very important in studies of cascading trophic interactions. Models, which offer great flexibility in the choice of time scales, were used to examine some of the likely consequences of cascading trophic interactions (Carpenter and Kitchell 1984, 1987). Two results from modeling proved especially useful in the design and interpretation of field studies.

When output of ecosystem models was sampled at regular intervals that mimicked typical limnological sampling regimes, correlations between variables were dependent upon the sampling interval (Carpenter and Kitchell 1987). For example, in a model in which phytoplankton dynamics depended on nutrient loading, nutrient recycling by grazers, and losses to grazing, the correlation coefficient of zooplankton biomass and primary production was a function of sampling interval (Fig. 1). When model output was sampled at certain time intervals, the correlation was positive. Some sampling intervals gave significant correlations, and other did not. When variables are known to be strongly related but a poor correlation is obtained, the investigator typically increases the sample size. However, it would often be more profitable to examine other time scales.

The analysis of dynamic systems by correlation without attention to time scale is likely to yield misleading results. It is easy to construct linear dynamic models in which two variables are functionally dependent but are uncorrelated at most scales (Chatfield 1980). Our experience with more complex and realistic models reveals poor correlations between functionally

related variables at certain sampling scales, including those commonly used by ecologists (e.g., weekly, monthly, annually, etc.). Moreover, correlations tend to be positive at certain scales and negative at others (Fig. 1). Such apparently conflicting results could lead to unproductive disagreements about the nature of the "true" relationship among the variables, when in fact both correlations are correct and the relationship is scale-dependent.

The second intriguing result that emerged from modeling studies concerned the relationship between zooplankton biomass and primary production. This relationship tends to be unimodal in the model results, with maximal primary production occurring at intermediate levels of zooplankton biomass (Carpenter and Kitchell 1984, 1987). Thus, under certain conditions grazers enhance primary production, while under other conditions grazers inhibit primary production. Because this unimodal relationship may complicate studies of food web-primary production interactions, it has been examined more closely using in-situ bag experiments.

THE UNIMODAL RESPONSE

An insightful experimental design for studying the effects of zooplankton on phytoplankton was introduced by Lehman and Sandgren (1985). Bags were filled with lake water from which the zooplankton had been removed by screening. A zooplankton gradient was created by adding different concentrations of zooplankton to a series of bags. Other bags received nutrient additions as well as zooplankton. After incubation for 2-5 days in situ, phytoplankton were collected from the bags. Net per capita growth rates were then calculated for each taxon using the initial and final algal concentrations. Degree of nutrient limitation and response to the zooplankton gradient were then determined for each algal taxon.

Four basic relationships between algal net growth rate and zooplankton biomass have been observed in such experiments (Lehman and Sandgren 1985; Bergquist and Carpenter 1986; Elser et al. 1987): (1) no correlation; (2) negative correlation; (3) positive correlations; and (4) unimodal relationship. Cases 3 and 4 occur only for taxa which are nutrient-limited. In these cases, enhancement results from nutrient recycling by the zooplankton. Results are dependent upon duration of the experiment, because positive responses (nutrient enhancement) take longer to develop than negative responses (grazing loss). Therefore, positive or unimodal relationships are observed in longer experiments but not in briefer experiments.

Collectively, these data suggest that the global response is unimodal (Fig. 2), provided the the experiment is long enough for growth enhancement to occur. Linear or nonsignificant responses are observed when the range of zooplankton concentrations used in the experiment is not broad enough to reveal the full unimodal response (boxes in Fig. 2). The response envinced by a particular algal taxon over a given range of zooplankton biomass depends on: the composition of the zooplankton assemblage, the other taxa present in the phytoplankton, depths at which the bags are suspended, and

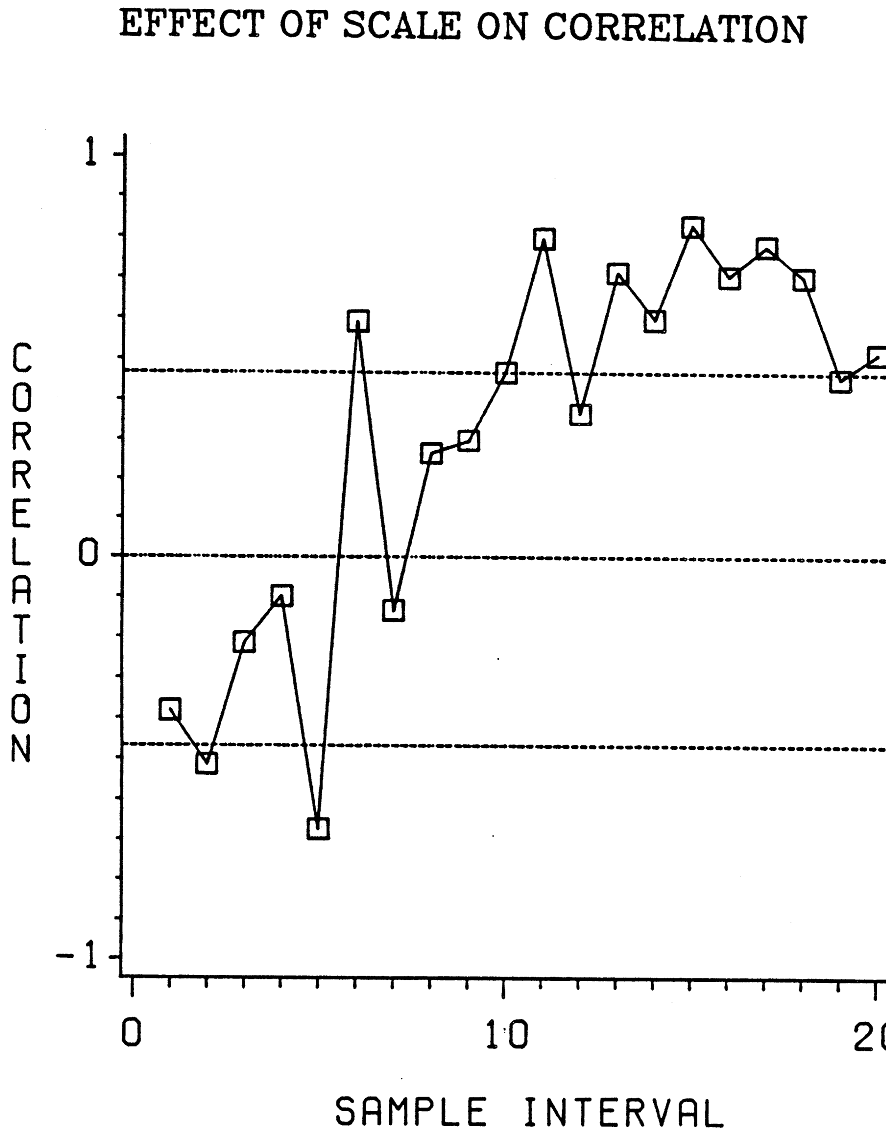

FIG. 1. Correlation of zooplankton biomass with primary production as a function of the time interval between samples. Correlation coefficients that lie outside the upper and lower dashed lines are significant at the 95% level.

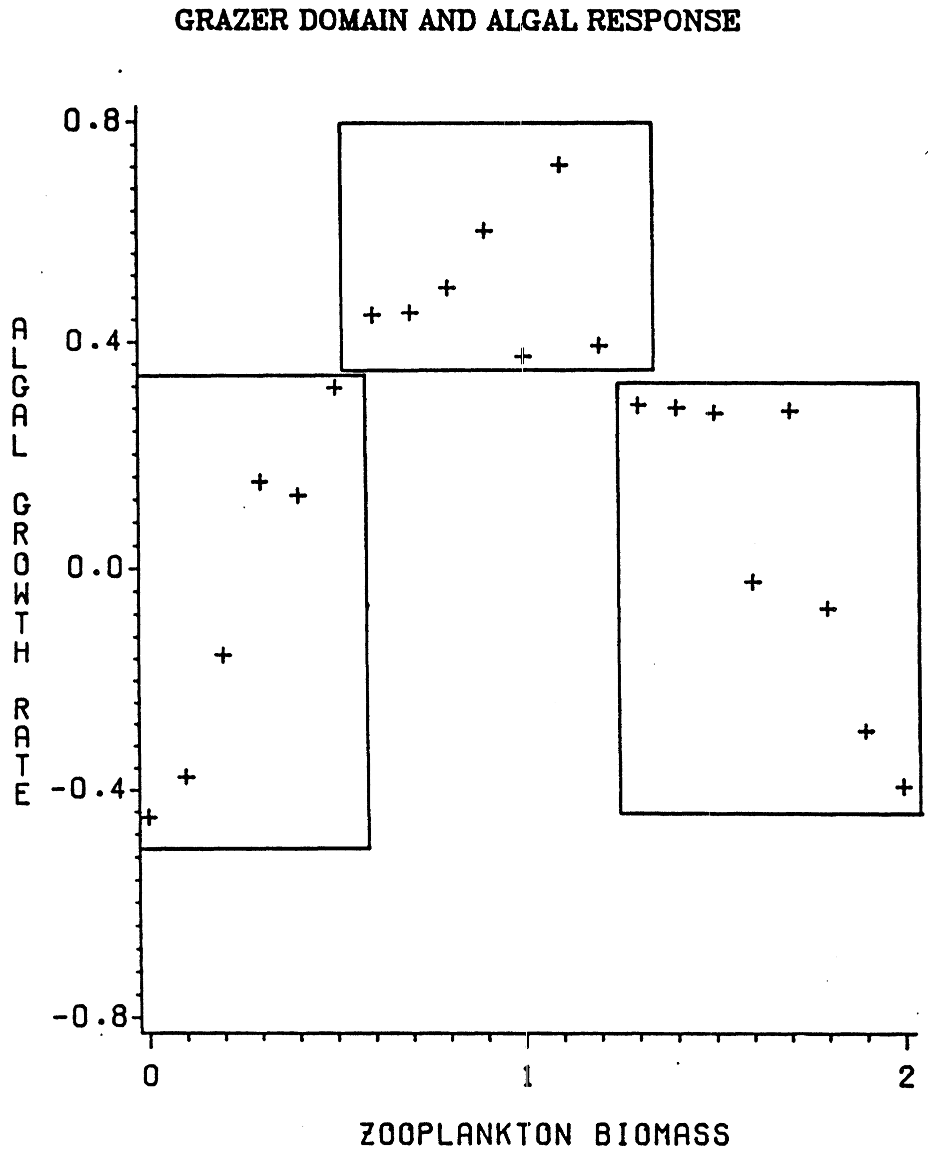

FIG. 2. Global relationship between algal growth rate and zooplankton biomass in bag experiments at a time scale of about 4 days and water temperature of about 20°C. Boxes enclose results of experiments using limited domains of grazer biomass, illustrating positive, nonsignificant, and negative responses.

the time of the growing season that the experiment is carried (Bergquist 1985; Bergquist et al. 1985; Elser et al. 1987; St. Amand and Carpenter, unpubl. data). If the composition of the zooplankton assemblage is specified, algal size is generally a good predictor of response to grazing (Bergquist et al. 1985). However, for certain phytoplankters other morphological or life-history traits are more important than size in determining the response to grazing (Bergquist et al. 1985; Elser et al. 1987).

Bag experiments generally confirm the relationships between zooplankton biomass, chlorophyll concentration, and primary production that emerge from models of the grazing process (cf. Carpenter and Kitchell 1984; Bergquist and Carpenter 1986). Certain species-specific responses, however, are not consistent with size-based grazing models (Lehman and Sandgren 1985; Bergquist et al. 1985; Elser et al. 1987). In any event, these relatively brief experiments do not address the issue of long-term stability and variability in the responses of phytoplankton to grazers. Dynamics at longer time scales have been investigated in whole-lake experiments.

WHOLE-LAKE EXPERIMENTS

Whole-lake experiments involved an undisturbed reference ecosystem, Paul Lake and two lakes, Peter and Tuesday, which were subjected to reciprocal fish exchanges (Carpenter et al. 1987a). Prior to manipulation, Paul and Peter lakes contained bass, which were principally piscivorous but ate some zooplankton. Tuesday Lake contained no piscivores prior to manipulation, but planktivorous minnows were abundant. Following a year of baseline study in 1984, reciprocal fish exchanges were carried out between Peter and Tuesday lakes in May 1985. 90% of the bass biomass of Peter Lake was moved to Tuesday Lake, and 90% of the minnow biomass of Tuesday Lake was moved to Peter Lake. We predicted that reduced zooplanktivory in Tuesday Lake would cause increased grazer biomass and reduced primary production. In Peter Lake, we expected that enhanced zooplanktivory would cause decreased grazer biomass and increased primary production.

Tuesday Lake's responses conformed closely to our expectations (Carpenter et al. 1987a). Pelagic fish populations were essentially zero within 2 weeks of the manipulation, as small fishes fled to littoral refugia and adult bass moved inshore to feed on them. In June and early July 1985, biomass of rotifers, small copepods, and *Chaoborus* increased. High densities of instar IV *Chaoborus* contributed to declining rotifer and copepod biomass after mid-July. Total grazer biomass, dominated by cladocerans formerly rare in Tuesday Lake, rose in late July. Initially, *Diaphanosoma leuchtenbergianum* was the dominant zooplankter, followed in sequence by *Holopedium gibberum* and *Daphnia pulex*. Phytoplankton composition changed dramatically, as formerly-dominant dinoflagellates disappeared. Dinoflagellate declines were consistent with results of bag experiments (Bergquist et al. 1985). However, fast-growing nannoplankton in Tuesday Lake were not strongly affected by the changes in the grazer community. Algal biovolume, chlorophyll concentration, and primary production declined as a result of the changes in the grazer assemblage.

The responses of Peter Lake were surprising and in some respects contradictory to our expectations: plankivory decreased because of unexpected behavioral responses of the fishes; herbivory increased; and productivity increased, but by unexpected mechanisms. The minnows added in May 1985 were eliminated from the pelagic zone within 2 weeks by a combination of predation by remaining bass and movement to littoral refugia. The large cohort of bass produced in 1985 remained in the littoral zone to escape cannibalism by adult bass. Adult bass, which consumed many Daphnia in 1984, were much fewer in number and distracted by other food items in 1985. Thus planktivory decreased, and the density and mean size of Daphnia pulex increased. The net effect of increased grazing and nutrient recycling by herbivores was stimulation of the phytoplankton. Algal biovolume, relative abundance of phytoplankton larger than 30 μm, chlorophyll concentration, and primary production increased steadily through the summer of 1985. The algae that accounted for these positive responses were gelatinous, colonial, grazing-resistant forms, especially Sphaerocystis schroeteri. Bag experiments and physiological indicators of nutrient deficiency showed that these phytoplankters were stimulated by increased biomass of zooplankton because nutrient excretion by herbivores alleviated nutrient deficiencies in the algae (Bergquist and Carpenter 1986; Elser et al. 1987; Elser et al. unpublished data).

Two fundamental ecosystem processes, primary production and nutrient cycling, were regulated by consumers in these experiments. Our studies were focused on the period of summer stratification, when effects of variable mixing regimes are likely to be minimized and food web effects are likely to be maximized. However, the summer is also the period of maximal ecosystem metabolism, and the period when public attention is fastened most closely on water quality. It is clear that any comprehensive assessment of lake ecosystem functioning or management must consider food web dynamics.

The results also demonstrate the importance of large-scale experiments: any system smaller than a whole lake would have given misleading results, because the responses hinged on the inshore-offshore movements of fishes. This leads to ambivalent conclusions about the reductionism-holism controversy in ecology. On the one hand, ecosystem dynamics depended on processes at lower levels of integration- the community and population levels. However, small-scale experiments alone may yield misleading inferences about ecosystem behavior, because too many contingencies are controlled by processes at larger scales. Our results are complemented by other examples of whole-system responses that were at odds with expectations derived from small-scale experiments (Carpenter and Lodge 1986). Small-scale experiments are helpful in showing which mechanisms are possible and how they work, but large-scale experiments are essential to tell which mechanisms are important.

INDICATORS OF ECOSYSTEM STATUS

In many lake ecosystems, and particularly in large lakes, it is difficult to perform controlled, large-scale manipulations or to match the intensity of sampling possible in small lakes. Where intensive monitoring is impractical, the best approach may be to focus sampling effort on a few integrative measures of system functioning. Whole-lake experiments will be useful for identifying such surrogates, describing their baseline variability, and determining their sensitivity to system-level changes.

At least two integrative, system-level indicators of food web change were clearly identifiable in our whole-lake results: cladoceran mean size and pheophorbide deposition rate. Cladoceran mean size was strongly responsive to zooplanktivory, and showed consistent negative relationships with chlorophyll concentration and primary production. Cladoceran mean size correlated more closely with algal biomass and production than did total zooplankton biomass or mean size, at both weekly and monthly time scales. Several well-documented allometric relationships suggest a strong functional link between cladoceran size and algal response (Carpenter and Kitchell 1984). Pheophorbide is a chlorophyll degradation product produced in the guts of crustacean grazers and degraded largely by sunlight (Welschmeyer and Lorenzen 1985; Carpenter et al. 1986). The pheophorbide deposition rate depends upon grazing rate and the efficiency with which grazer feces can sink out of the photic zone (Carpenter et al. 1987b). Both cladoceran mean size and pheophorbide deposition rate can be monitored using sediment traps, or historical records can be reconstructed from cores of the sediment.

Lake Michigan provides one example of a massive food web change reconstructed from the paleolimnological record (Kitchell and Carpenter 1986). Indicators used in this case were pheophorbide deposition and the mucron length of *Bosmina*. The latter is dependent upon the abundance of *Bosmina*'s invertebrate predators (Sprules et al. 1984). Following the irruption of alewife in Lake Michigan, mucrons of *Bosmina* became much shorter while pheophorbide deposition increased substantially in the sediment record (Kitchell and Carpenter 1986). By combining the paleolimnological data with scattered historical information and a model of pheophorbide deposition, the following causal sequence was deduced (Kitchell and Carpenter 1986). Declining densities of piscivorous fishes allowed alewife populations to increase. Increased zooplanktivory reduced the body size and biomass of cladoceran grazers, and decreased the biomass of copepods predatory of *Bosmina*. Consequently, the length of *Bosmina* mucrons declined. Metalimnetic diaptomids became the dominant grazers. Total grazing rates declined. Because grazing was reduced, algal biomass increased and transparency declined. Pheophorbide deposition increased because fecal particle size increased, the locus of grazing shifted to the metalimnion, and transparency declined. All of these factors decreased the photodegradation of the pigment. The reduction in the rate of photodegradation of pheophorbide far exceeded the reduction in its rate of formation due to reduced grazing. Therefore, the deposition rate of pheophorbide increased. More recent changes in Lake Michigan, including increased piscivory by introduced salmonids, the decline of alewife, and the return of large

daphnids (Kitchell and Crowder 1986; Scavia et al. 1986), prompt the prediction that Bosmina mucrons will lengthen and pheophorbide deposition rates will decline (Kitchell and Carpenter 1986).

SCALE AND DETAIL

The various approaches to lake ecosystem research differ in the time scales which they address as well as their degree of realism, detail, and/or complexity (Fig. 3). All models employ simplification to achieve insight, and so are low in realism, detail, and complexity. However, models offer great flexibility with respect to time scale. Laboratory microcosms achieve somewhat greater realism than models, but generally operate on restricted time scales of hours to months. A similar range of time scales is addressed by field mesocosms, which offer relatively great realism, detail, and complexity. Whole-ecosystem results are the standard of realism, detail, and complexity to which all other approaches must be compared. However, whole-system studies at time scales greater than a few years are rather rare (Strayer et al. 1986). Paleolimnology is the only consistent source of data at time scales of decades to centuries. Paleolimnological data span a great range of levels of realism, detail, and complexity (Binford et al. 1983).

Aquatic ecologists are asked by society to provide information for management decisions that usually focus on time scales of years to decades. Models, paleolimnology, and whole-system studies are the only approaches that directly address these time scales. However, a number of constraints on whole-system studies dictate important roles for microcosms and mesocosms as well. Multiple causality operates in ecosystems, and small-scale reductionist experiments are necessary to separate and quantify contrasting causal mechanisms (Hilborn and Stearns 1982). Yet, small-scale studies alone are not sufficient for forecasting whole-system response, because they cannot determine which of the various causal pathways will predominate at the ecosystem level. One of the great challenges of ecology is to understand how information from models, small-scale experiments, and paleoecology can be translated into inferences and predictions about ecosystem response.

Comprehensive whole-system studies are complicated, costly undertakings. Therefore, they will not be common. Whole-system experiments will be even rarer. Several solutions are conceivable for this dilemma. One necessity is the development of readily-monitored indicators that provide certain integrative information about ecosystem status, as discussed above. A possible research strategy is to punctuate long periods of conservative ecosystem management with occasional episodes of a radically different protocol, to assess system response to contrasting management techniques (Walters 1984). Still other approaches might blend models, mesocosms, and paleolimnology to forecast system behavior. An important issue for this meeting is to determine methodologies and priorities for using limited information to make inferences and forecasts about large, complex ecosystems.

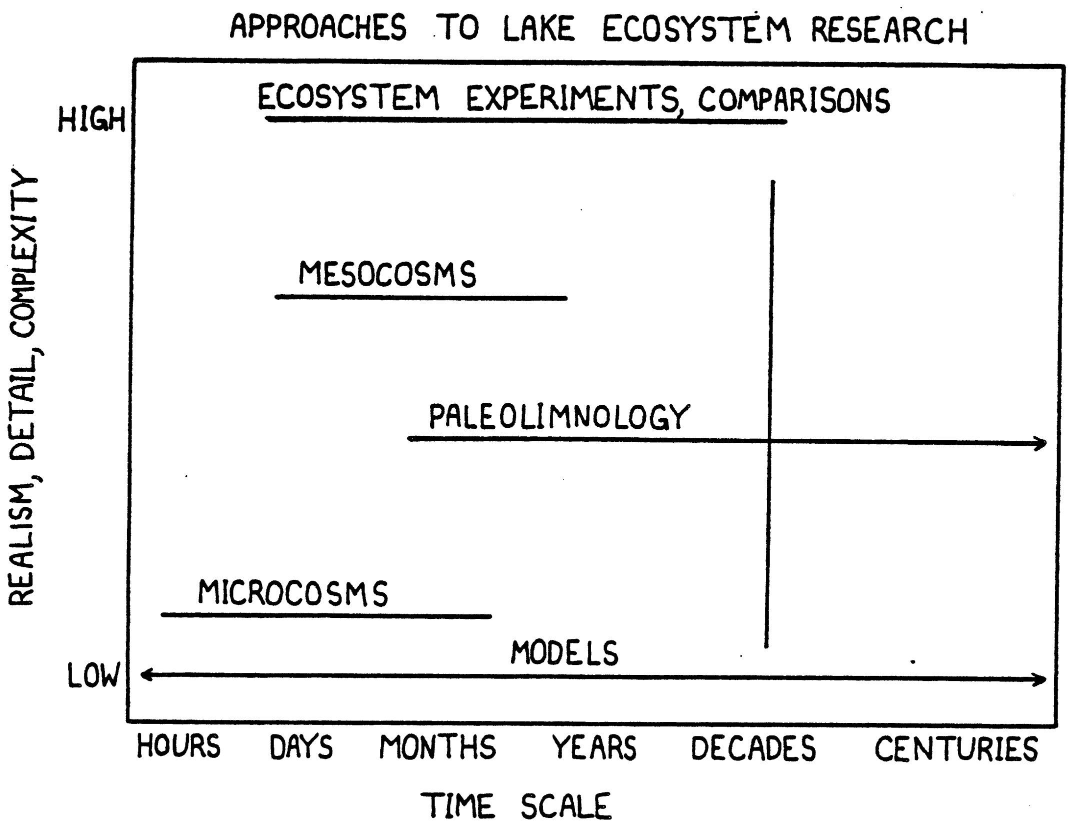

FIG. 3. Approaches to lake ecosystem research, ordained on the basis of time scale and degree of realism, detail, and/or complexity. See text for further description.

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APPENDIX B5

FOOD WEBS AND COMMUNITY STRUCTURE

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Since the Laurentian Great Lakes are intermediate in size between small lakes and oceans, it is not unreasonable to assert that community-level research approaches in the Great Lakes must in some manner combine methodologies suited to large and small aquatic ecosystems. In smaller lakes where numbers of species are lower and physical scales are tractable, enclosure experiments, whole-lake manipulations, and detailed analyses of food webs are feasible. By contrast, in oceans where physical scale is enormous and species numbers can be great, emphases on experimentation and detailed species analyses are largely, but not exclusively, abandoned in favor of energy flow and production studies based on rather coarse groupings of living organisms (trophic levels, "trophospecies," size, etc.).

WHAT QUESTION ARE WE ASKING?

Clearly it is not possible to establish methodology until a scientific hypothesis or objective is formalized. In this paper I will comment on basic issues in Great Lakes research relating to food webs and community structure. I will asssume our goal is to model interactions within communities well enough to be able to predict how these communities will respond to perturbations such as nutrient loading, contaminant additions, harvesting practices, and species additions and deletions, particularly in relation to resultant effects on harvestable fish production. My intention is to describe a comparatively new tool for the study of aquatic communities, the biomass size spectrum, and to discuss its strengths and weaknesses relative to some other general approaches. I will conclude by suggesting that this methodology deserves serious attention in the Great Lakes context because it is a community-level approach that can easily be related to some promising species-level models.

BACKGROUND

Unfortunately the original empirical observation by Sheldon et al. (1972), that in pelagic communities the biomass in logarithmic intervals of organism size is roughly the same from bacteria to whales, has come to dominate most people's general perception of these ideas. Description of empirical patterns in particle-size distributions (Fig. 1), while initially useful, is no longer of primary importance. Models of the biomass size spectrum and biomass flow through a food web have advanced enormously since Sheldon's pioneering work. They are at the stage now where they can make significant contributions to modeling and managing the Great Lakes (Sprules et al. 1983; Sprules and Munawar 1986).

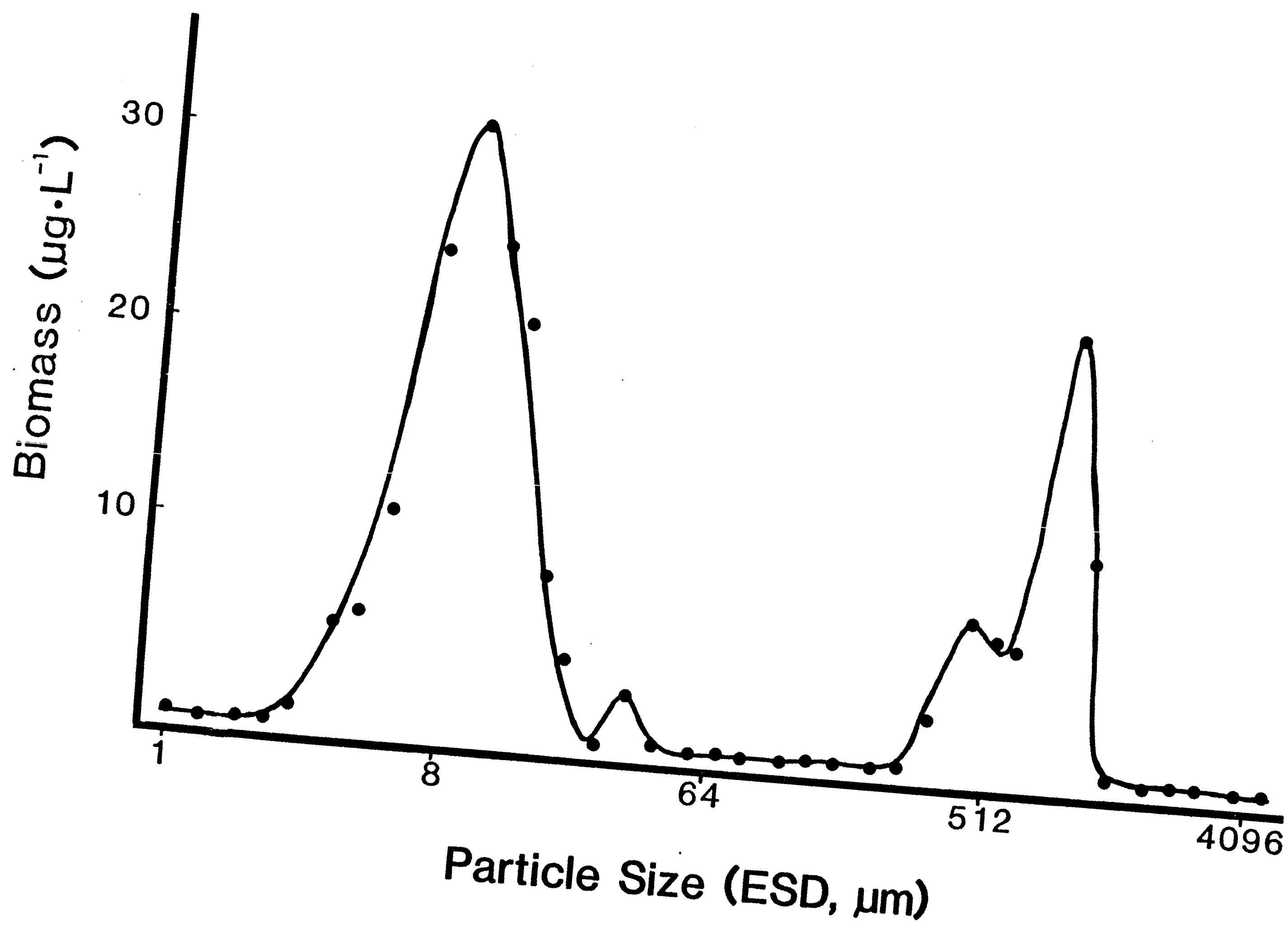


FIG. 1. Plankton size spectrum from an inland lake. ESD = equivalent spherical diameter.

THEORY

In their simplest form, models of biomass distribution in aquatic communities derive from the approximation that production of a predator population is given by production of the prey population times the predator's growth efficiency corrected for uningested prey production (Fig. 2). Furthermore, P/B or turnover ratios are strongly size-dependent (Banse and Mosher 1980), so that one can derive an expression for biomass ratios in adjacent trophic levels (Fig. 2). A unique feature of pelagic communities is that predator/prey size ratios are relatively invariant (Sheldon et al. 1977), exploitation efficiencies are close to 100%, and growth efficiencies are known generally (Kerr 1974). This leads to the conclusion that biomass ratios of adjacent trophic levels should be close to unity for reasonable ranges of values of growth efficiency and exploitation efficiency (Fig. 2). Sheldon et al. (1977) used these concepts to estimate an annual sustainable yield of the anchoveta fishery off the coast of Peru of 10 million metric tons, which compared with actual landings ranging from 8.5 to 12.3 million metric tons.

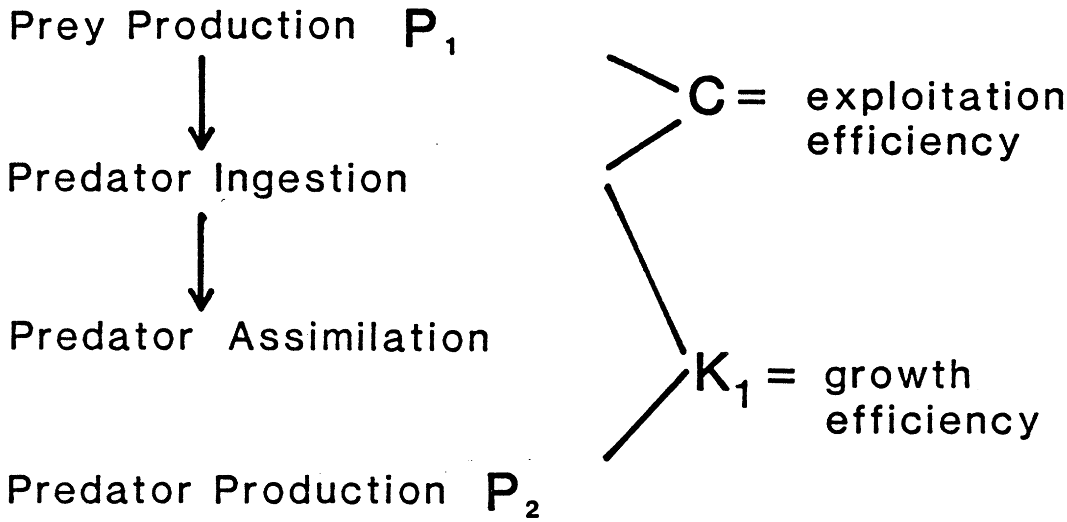
The difficulty with this simple version of the model is that it is based on trophic levels, which are often "blurred" into food webs (Kerr 1974). It worked for the Peruvian anchoveta fishery because energy flow to the fish was relatively direct from zooplankton. Borgmann (1982) has circumvented this difficulty by introducing the concept of particle-size conversion efficiency, e, in place of trophic-level conversion efficiency K_1, thereby permitting computation of biomass conversion from one size to another independent of trophic level (Fig. 3). The basic equations that comprise this version of the model are

$$P_{xy} = d(W_y{}^{-e} - W_x{}^{-e})$$

$$P/B = aW^{-n}$$

$$B_{xy} = b(W_y{}^{n-e} - W_x{}^{n-e})$$

where P, B, and W are production, biomass, and body mass, respectively, x and y are size limits, and n, d, a, and b are fitted constants. They permit estimation of production within any size range of organisms provided data on production at some other size range are available (Table 1). Borgmann et al. (1984) used this approach to estimate potential production of fish in Lake Ontario from detailed data on zooplankton production. One can also predict patterns in the distribution of biomass in different size ranges of organisms for a given lake (Minns et al. 1987; Fig. 4). The important assumptions of this version of the model are (a) nonpredatory mortality is negligible, (b) all prey production is consumed by predators, (c) the predator/prey size ratio is constant, and (d) the system is in steady state.



$$P_2 = P_1 \times C \times K_1$$

$$P/B = aW^{-n}$$

$$B_2/B_1 = (W_2/W_1)^n \times C \times K_1$$

$$\approx (3000)^{0.24} \times 1 \times 0.15$$

$$\approx 1$$

FIG. 2. Simple version of a particle-size model. P, B, and W are production, biomass, and body mass respectively. n and a are fitted constants.

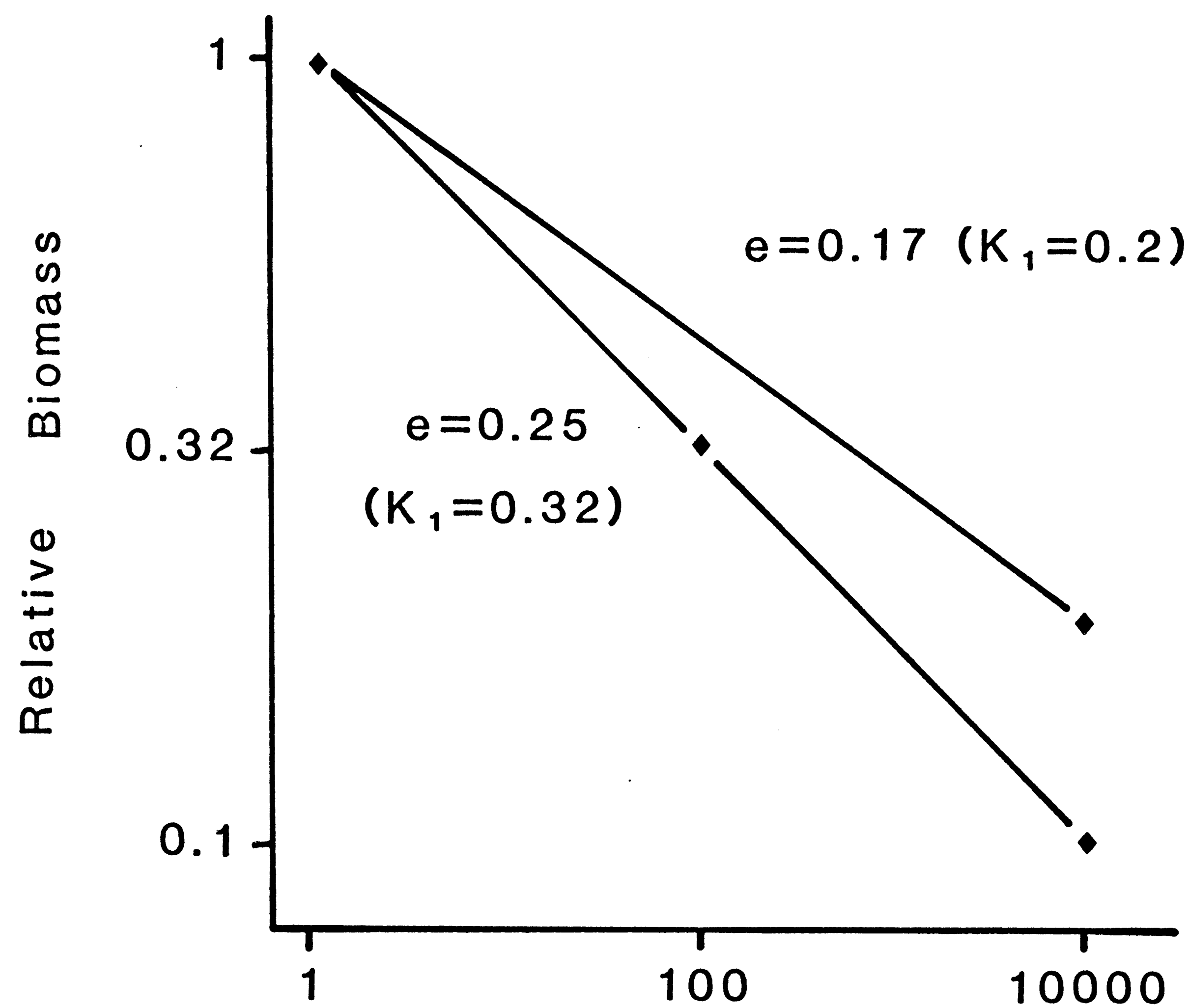


FIG. 3. Illustration of e (particle size efficiency). Top line is for predators of size 10000 consuming prey of size 1 with a growth efficiency of 0.2 (K_1) in a single trophic step. Lower line includes an intermediate second trophic level and growth efficiencies at each step of 0.32. Adapted from Borgmann (1982).

TABLE 1. Example of calculation of fish production in Lake Ontario from zooplankton production. Adapted from Borgmann (1987).

Zooplankton mass (W_x, W_y)	10^{-7} to 10^{-2} g dry wt
Zooplankton biomass	2.4 $g.m^{-2}$
Zooplankton turnover	$18.yr^{-1}$
Zooplankton production P_{xy}	43 $g.m^{-2}.yr^{-1}$
e	-0.26
d	$P_{xy} / (W_y^{-e} - W_x^{-e}) = -1.24$
Fish mass	50 to 600 g dry wt
Fish production	$-1.24 \ (600^{-0.26} - 50^{-0.26})$ $= 0.21 \ g.m^{-2}.yr^{-1}$

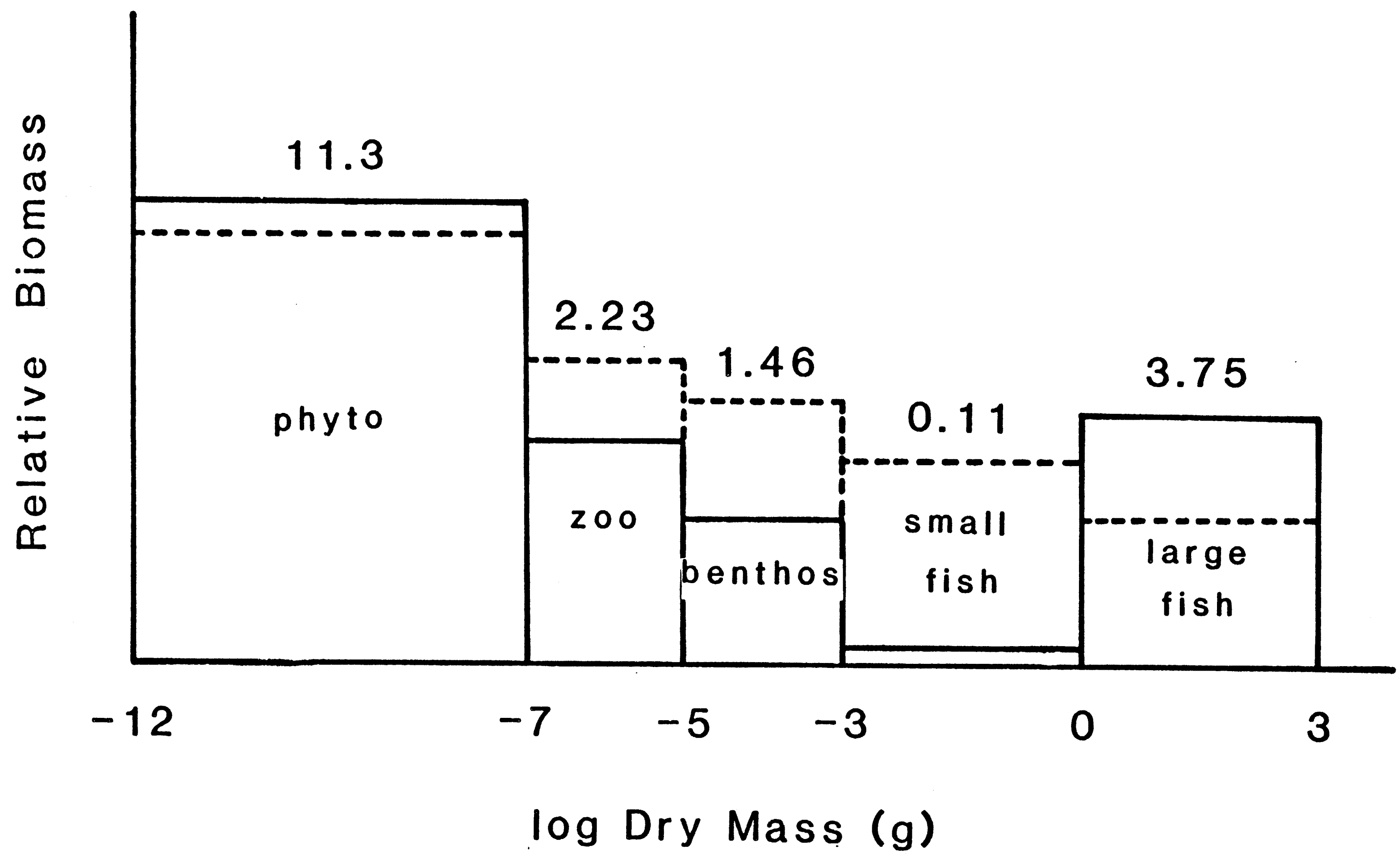


FIG. 4. Biomass distribution for the Bay of Quinte, Lake Ontario, computed using Borgmann's model. Solid bars are observed, dashed are predicted values. Numbers above each bar are total observed biomasses in each group. Adapted from Minns et al. (1987).

APPLICATIONS

The foregoing is a simple, but adequate, description of a model of biomass distribution for purposes of illustrating its utility in the Great Lakes context. Perhaps most importantly it can be used to predict production of a particular size or size range of organisms as long as e is constant and known for a particular lake, and if an estimate of production for some other known size range of organisms is available (Borgmann et al. 1984). So, for instance, the production of a population of particular-sized fish could be estimated from knowledge of invertebrate (Borgmann et al. 1984; Table 1) or algal production within known size limits. The required information is much less detailed and costly than that needed for detailed population dynamics models. The constancy of e for a particular lake is assumed, but Borgmann (1982) showed that this is at least as justifiable, if not slightly more so, as the assumption of constant growth efficiencies (K_1) in more traditional energetics models.

The model can also be used to predict the shape of the biomass distribution of organisms in a lake for any particular size groupings of organisms (Fig. 4). Minns et al. (1987) argue that nutrient supply rates to a lake set the total biomass and potential transfer of production up the food web. The body-size dependent ecological interactions among organisms that are embodied in the biomass model then determine the allocation of biomass among size groups. Typical values of n^{-e} (see equations above) are usually slightly less than 0, and this defines a monotonically decreasing biomass spectrum near steady state (Fig. 4). If trophic interactions are disturbed through overexploitation of some species, or through introductions of exotic predators, some segments of the spectrum will decrease while others compensate. These imbalances will be apparent through analyses of actual versus predicted biomass distributions.

Particle-size conversion efficiency is also related to the efficiency with which contaminants such as mercury, PCBs, and DDT are transferred through the food chain (Borgmann and Whittle 1983). Knowledge of body burdens of contaminants in organisms of known size permits the estimation of parameters necessary for predicting contaminant concentrations in organisms elsewhere in the food web. So, for instance, the concentration of such contaminants to be expected in a newly stocked fish species could be determined from adult size and the above parameter values.

ADVANTAGES OF BIOMASS MODELS

The principal advantage of the biomass size model is that it encompasses all organisms in an aquatic food web, from picoplankton of less than 2 μm to fish of 1 m. Production and biomass of this tremendous range of living organisms can easily be catalogued or projected from comparatively simple information within a single model. All of the component processes in the model - growth, predation, energy transfer - are strongly size-dependent. Food web models based on species are typically restricted to dealing in detail with only a few species, often within a single trophic level. Thus the interesting work of Crowder et al. (1987) and Kitchell and

Hewett (1987) on recent trends in the Lake Michigan pelagic community is restricted to a handful of fish species and one or two dominant zooplankters. It would be prohibitive to quantitatively measure and represent interactions amongst hundreds, scores, and tens of algal, zooplankton, and fish species, respectively, by considering individual species.

One of the major themes emerging from this workshop on large lakes is the opportunity available for comparative studies. The Laurentian Great Lakes are large and relatively young, the African Rift lakes are large and old, oceans are even larger and older. This opportunity has generated questions such as - Are the plankton communities of ancient lakes more highly coevolved and hence energetically more efficient than those of younger lakes? Biomass size models are particularly well suited for initial studies of comparative plankton community structure among such lakes. Size data are comparatively easy to obtain so that major variation in community structure can be quantified with minimum effort. Furthermore, ratios of biomass in adjacent trophic levels provide a rough indication of efficiency of energy transfer. It is my view that a useful initial step in broad-scale comparisons of aquatic community structure would be the construction and analysis of biomass spectra.

Biomass models permit quantitative prediction of production for any-sized organisms from comparatively simple data. Of course it is the prediction of fish production that is most relevant in the Great Lakes context. Expected production for just the specific size class within a species that is normally the target for a fishery, ignoring production of other life stages of the species, can be computed.

Collection, and especially processing, of routine monitoring data on the biota of the Great Lakes would be greatly facilitated through application of size concepts. Phytoplankton samples could be processed on board ship through an automated sizing device such as a Coulter counter. Zooplankton could be detected acoustically, or sampled traditionally and automatically sized in the laboratory with computer imaging techniques. Fish can be sampled acoustically in situ. With some effort these practices could become routine, and resultant data plotted as a biomass spectrum soon after the completion of a cruise. Such spectra would provide continuing reference data on community structure, and provide a basis for quick recognition of change in structure that could be caused by, or even presage, an important trophic perturbation such as excessive forage demand by a rapidly growing piscivore population.

DISADVANTAGES

So much of our tradition, especially information required by fisheries personnel, is steeped in the species tradition that a model formulated solely on the basis of size will be perceived to have limited scope. Interest is not in the expected production of 10 kg fish, but rather in adult lake trout or coho salmon. This is a limitation. In terms of expected trends in, say, Lake Michigan, the interest is in whether alewives will disappear, or whether _Daphnia pulex_ will rapidly increase, or whether

Mysis will decline, not in shifts in overall size distributions. The work by Crowder and Kitchell cited above is, in this sense, more relevant despite its more retrospective than prospective form. They understand why alewives are declining (increased forage demand by salmon) and why *D. pulex* is increasing (alewives declining) but cannot predict very quantitatively future species shifts. Kitchell et al.'s (1977) bioenergetic approach, on the other hand, permits more precise prediction based on known growth rates, forage demands, mortality, etc. of a given fish species. It is interesting to note that Lake Michigan started with a lake trout and native herring community about 100 years ago, and 100 years from now may have a (managed) salmon and alewife/smelt community. My personal guess is that, in terms of size-specific production and biomass the two communities may not differ substantially. The players differ but the roles do not. This way of thinking, and a reasonably quantitative prediction, derives from a size perspective, not a species one. Whether a community has changed or not depends very much on how its structure is measured.

Thus, while size models can make generalized predictions about community structure independent of species changes, food web or bioenergetic models can make some projections about individual species. Here is the opportunity for combining the two approaches to advantage. The expected production of particular sized organisms generated by size models can possibly be apportioned among particular species by the food web or bioenergetic models. There is much common ground between bioenergetic and size models because they are both based on energy processes such as growth and predation. Clearly there is considerable opportunity here for combining the approaches in a manner that will significantly enhance our capacity for projecting future trends in the Great Lakes.

All models have assumptions, so those of the biomass size approach may not be any more or less serious than others. Certainly the assumption of near steady-state conditions will be difficult for many who are constantly dealing with seasonal and annual variation in Great Lakes communities. Moderate-term averages against a background of annual or seasonal "noise" may nevertheless be worth considering, and these might be close enough to steady-state for our purposes. The constancy of size- dependent parameters for all sized organisms is only an approximation, as is the constancy of the predator/prey size ratio, and the notion that all prey production is consumed by predators. I will suggest below that many of these assumptions could possibly be relaxed in an expanded version of the model.

The size model described here is very much restricted to pelagic communities, a restriction that makes no sense in shallow lakes such as Erie where close coupling with littoral and benthic communities undoubtedly occurs. Perhaps in the open waters of Lake Superior this ideal is more closely approximated, and application of the model should be more successful. One could consider size models to be null pelagic models, and that deviations from it are at least partially reflective of the importance of linkages to these other communities.

PROGNOSIS

The version of the size model I have discussed here subsumes many size-dependent processes such as metabolism, respiration, somatic growth, and reproduction as well as efficiencies of assimilation and exploitation. It should be possible to develop a more detailed form of the model that incorporates such processes throughout the food web more explicitly (e.g., Silvert and Platt 1980). Such a detailed model would permit sensitivity analyses to determine which parameters most seriously influence the model's behavior, and hence which ones have to be estimated most carefully. This would facilitate the development of more specific predictions, and provide answers to the following sorts of questions. How would harvesting a given size range of fish at a particular rate affect the production and biomass distribution in a pelagic community? How would such a community change if a whole size group of organisms migrated elsewhere (e.g., the change in adult bloater from a pelagic to benthic existence in Lake Michigan), thus creating a "hole" in the size continuum? How would a 1 mm shift in the mean size of zooplankton affect energy flow and community structure in the system? How would a community respond to a program of stocking fish that would add biomass in particular size categories?

These are the sorts of questions researchers are likely to ask of the Great Lakes. Preliminary answers are derivable from current versions of size models, and more detailed ones would follow from elaboration of the models. It is my view that this development can be an exciting and productive addition to the arsenal of tools we bring to Great Lakes research. The approach, though, should not be applied in isolation, for clearly insight into large lakes will not be thorough without concomitant species-specific information on trophic interactions and behavior.

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